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Evolution of the Color Pattern in
the Microlepidopterous Genus
Lithocolletis

BY
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I. INTRODUCTION.

The interest in a study of the origin of the many and complex forms of color pattern in insects lies mainly in the hope that such a study may give additional insight into the fundamental principles of evolution in general. With few exceptions, such as the work of Tower on *Leptinotarsa*, researches of this nature have been confined to the Macrolepidoptera, chiefly to the butterflies and higher moths. The Microlepidoptera, which are less advanced from the viewpoint of evolution, have been almost neglected. Yet, within this group, several of the older and larger genera afford excellent and ample material for such an investigation. To secure convincing data, a critical study, both ontogenetic and phylogenetic, must be made of the species of a large genus, in which the color patterns, while sufficiently diverse to indicate that a considerable degree of evolution has taken place, are still comparatively simple.

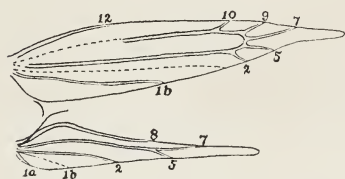
The genus *Lithocolletis* fulfills to an extraordinary extent these requirements; hence the following investigations were undertaken with the object of ascertaining the modes of origin of the various color patterns in this genus and the influences which have been operative in their evolution. The study of adult color patterns has extended over a period of several years; the observations on pupal development were made during the summer of 1910.

It is a pleasure to express to Prof. M. F. Guyer my appreciation of his many helpful suggestions during the progress of my work.

II. METHODS AND OBSERVATIONS.

(a) SYSTEMATIC POSITION AND CHARACTERISTICS OF LITHOCOLLETIS.

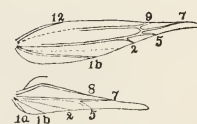
The genus *Lithocolletis* belongs to the large family Tineidae of the Microlepidoptera. It comprises a large number of very small moths, varying in expanse from 4 to 12 millimeters. The larvæ are exclusively miners, usually in leaves or very rarely in the bark of stems. The entire larval and pupal existence with one or two exceptions is passed within the mine. The genus, as originally established, has a remarkably uniform structure and a very characteristic appearance, enabling one to recognize the species easily. The structural characteristics which distinguish the typical and principal group are the following:

FIG. 1. Venation of *Lithocolletis*.

Face smooth; crown tufted; labial palpi porrected or drooping, moderately long and pointed; maxillary palpi rudimentary; tongue of moderate length; antennæ nearly attaining the wing length, simple in the male, basal joint thickened and bearing a pecten. The forewings are elongate, lanceolate, acuminate. The hindwings are about one-half the

breadth of the forewings, linear lanceolate and fringed with cilia whose length is from four to five times the breadth of the wings. The venation is illustrated by *Fig. 1*;¹ forewings, 1b simple, 3 absent, 4 absent, 6 absent, 7 to costa, 8 absent, 11 absent; hindwings, 3 absent, 4 absent, transverse vein absent between 2 and 5, 6 absent. The posterior tibiæ bear appressed hairs.

All of the European species and the great majority of the American species conform to the above conception of the genus. There are, however, in North America a few species belonging to two different groups, which differ structurally from the typical species; for these, two subgenera, *Porphyrosela* and *Cremastobombycia* have been erected (Braun, '08). The former of these, *Porphyrosela*, differs from *Lithocolletis* in the absence of vein 10 of the forewings, the absence of a pecten on the first joint of the antennæ and in the absence of hairs on the hind tibiæ.² It thus represents a later development, phylogenetically, in the direction usually taken in this family; that is, a reduction in the number of veins (*Fig. 2*). *Cremastobombycia* is of a more ancestral type than the typical *Lithocolletis*; it possesses an additional vein in each wing; on the forewing, vein 4 is present and stalked with 5; on the hindwing, vein 6 is present and long stalked with 5 (*Fig. 3*).

FIG. 2. Venation of *Porphyrosela*.

In the European fauna, the typical Lithocolletids are a very homogeneous group of species both as regards larval characteristics and imaginal markings.

¹References in italics are to the text figures, those in Roman type to the figures on the plates.

²Since this paper was written, studies on very closely allied species have shown that these characters are not sufficiently constant to define a genus (Meyrick, *Genera Insectorum*, 128me Fascicule, p. 5, 1912). Vein 10 is probably faintly visible in large specimens of *L. desmodiella*.

In all, the larva is of the so-called cylindrical type, which agrees well with the usual type of lepidopterous larva. During the first three instars, in which the extent of the mine is gradually increased by a loosening of one epidermis, the larva has a characteristically flattened shape, with flat head and projecting mouth-parts. After the third moult, the larva assumes the normal cylindrical shape and the mine becomes tent-like by a fold in the loosened epidermis. The larva then consumes the greater part of the parenchyma within the area occupied by the mine. The pupa, except that of one species, is always formed within the mine and may or may not be enclosed in a cocoon.

The forewings of the imagoes are marked by various combinations of white transverse fasciæ and streaks on a yellowish ground color. These white marks are bordered along their inner edges by dark brown or blackish scales; sometimes, but to a less extent, dark scales may also appear along their outer edges. The hindwings are unicolorous.

Our American species while conforming in all structural characteristics to those of Europe, fall naturally into two groups; one of these agrees closely in structure of larva and imaginal markings with the European type just described; the other has what has been termed the "flat larva," and the imagoes produced from such larvæ can always be sharply distinguished by their markings from the species of the "cylindrical-larval group." The "flat larva" retains the flat shape, which is characteristic of the first three instars of the "cylindrical-larval group," through the fourth, fifth and sixth instars, only assuming the cylindrical shape and an approach to normal mouth-parts with the last moult. By some systematists, the persistence through three additional larval instars of the curious modification of the mouth-parts, which is in fact an adaptation for loosening the epidermis, has been regarded as a sufficient ground for the generic separation of this group, and the name *Cameraria* Chapman has been applied to it (Chapman, '02). The other view, which regards the modification of the mouth-parts merely as an adaptation for a particular mode of life, and not a character indicating the natural separation of that group from one with which the imagoes agree in all structural details, has been presented in the *Canadian Entomologist* for December, 1909 (Braun, '09).

The mines of the "flat-larval group" are always found upon the upper side of the leaf. The increase in the extent of the mine continues through six instars, the larva consuming only a few layers of cells in front of it. For this reason, the parenchyma within the mine is never entirely consumed and the mine rendered semitransparent, as is the case in mines of the "cylindrical-larval group." During the seventh instar, the larva does not feed; the time is occupied in preparation for the pupal state. Where the imago is to emerge the same summer, most of the species spin cocoons. The cocoon is a flat, oval sheet of silk attached around its edge to the floor of the mine, the epidermis above being

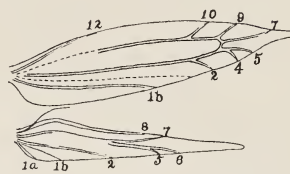


FIG. 3. Venation of *Cremastobombycia*.

thrown into a fold. In the overwintering generation, the larvæ hibernate, changing to pupæ in spring without spinning cocoons. The characteristic which distinguishes the imagoes of this group from the usual type is that the dark scales appear on the outer edges of the white streaks and fasciæ; if a margin is present on an inner edge, it is much less pronounced.

The wide geographical range and the large number of species would lead to the inference that the genus is an old one. If so, we would expect to find some species which have halted at an early stage in their evolution and have therefore preserved a color pattern which should bear some resemblance to the primitive one and hence afford a clue to it. Others would have advanced farther, development ceasing at different levels, so that the numerous differentiations produced should constitute a chain of related species, broken no doubt by numerous gaps but still sufficiently complete to indicate the different directions which evolution has taken. The problem of this research is, then, to determine what is the primitive color pattern of this group and knowing it to trace the paths along which evolution has proceeded in the production of the respective patterns of the numerous species now in existence. It is scarcely probable that the primitive pattern is preserved among any of the earlier genera from which *Lithocolletis* is descended. Such a long period of time has elapsed since the origin of *Lithocolletis* that the species now belonging to ancestral genera have probably deviated widely from the type of marking then characteristic of them. This view is rendered more plausible by the fact that the subgenus *Cremastobombycia*, which possesses structural generic characters which suggest it as the immediate ancestor of *Lithocolletis*, has a type of marking differing considerably from that common to the large and widely distributed typical group and resembling, to a marked degree, the type of marking characteristic of some of the species of the smaller and seemingly younger group, usually known as the "flat-larval group." If so, we should search for the primitive color pattern among the less differentiated species of the typical group of *Lithocolletis*.

If evolution takes place in several definite directions irrespective of utility, as contended by Eimer, this group should offer an opportunity of testing this theory, within certain limits, since many of the highly specialized differentiations, indicating a high phylogenetic development and requiring a long time to perfect, are of almost microscopic proportions and of no conceivable value in the life of the organism. Hence it is improbable that natural selection would have stepped in to mar any results which might have been produced through orthogenesis.

In a genus such as this, where the color combinations are relatively simple and the limits of the marks clearly defined and the pigmental colors belong to the single series of yellows (or reddish yellows), browns and blacks, the problem of tracing their differentiation both ontogenetically and phylogenetically should be one less complicated than in higher groups, and the observations should offer more direct testimony as to the means by which such results are obtained.

(b). COLOR CLASSES REPRESENTED AND STRUCTURE OF SCALES.

Tower ('06) has given a comprehensive survey of the literature dealing with the production of color in insects. Merely a brief summary of the salient facts bearing on the subject of this research is given below, and the reader is referred to the researches of Tower and earlier investigators for a complete statement of what has been accomplished along this line. This author has divided the colors of insects into three main classes, based upon their means of production. These are chemical or pigmental, physical or structural and chemico-physical or combination colors. Pigmental colors are further subdivided into three groups: cuticula or dermal, hypodermal and subhypodermal colors. The pigments through whose agency colors in the scales of Lepidoptera are produced are largely hypodermal; though there is a possibility that certain browns and blacks, which are very permanent under the influence of reagents, are cuticula colors and therefore located in the walls of the scales, instead of being present as granules within the scales. White is probably the only purely physical color in insects, although various other colors may be produced through the agency of physical causes acting in combination with pigments. The latter, the chemico-physical colors, are the most widely distributed and are due to the action of light falling upon a surface of different structural modifications over a layer of pigment. The various lustrous, metallic and iridescent colors of scales of Lepidoptera are due to this cause.

In the group under consideration, the lustrous white of the streaks and fasciæ is produced entirely through structural agencies. The scales over these areas, when tested by the addition of alcohol, cedar oil or other similar reagents—a method originated by Dimmock ('83),—are rendered transparent and colorless, proving that these scales are hollow and contain no pigment. The shining golden yellows, browns, black and iridescent blues are combination colors. When viewed by transmitted light, the scales reflecting the first three of these colors remain essentially the same color; the iridescent blue scales appear to contain a pale brown pigment; hence the blue is entirely due to physical causes.

The scales in the majority of the species have a remarkably uniform structure and shape, although showing great variation in size and in the proportion of length to breadth. In any one of the typical species, *L. lucidicostella* or *cratægella* for example, the scales are wedge-shaped, tapering more or less rapidly to the short stem by which they are inserted into the wing. The outer edge of the scale is dentate, the number of teeth varying from two or three in the elongate scales around the apex of the wing in the cilia to seven or eight in the broader and shorter scales lying over the wing membrane. In some of the scales, the teeth are approximately equal; in others, they are of uneven sizes, and a small tooth is sometimes inserted between two larger ones. Variations in the shape of scales over the main part of the wing are illustrated by *Fig. 4*. The last row of scales projecting from the apex of the wing over the cilia is composed of

exceedingly elongate, linear scales, so that toward their bases they appear almost as fine as the cilia themselves. Such a scale, one of the blue iridescent scales in the cilia of *L. cratægella*, is illustrated by *Fig. 5*. The scales forming the apical spot, a characteristic of a considerable group of species, are smaller than the average and proportionately broader and are of almost uniform size. The scales in the black patch before the apex of such species as *L. cratægella* are very similar to these.

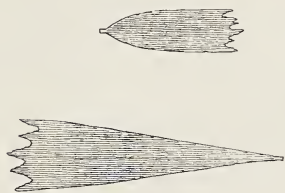


FIG. 4. Wing scales.

All of the scales just described are marked with a series of nearly parallel striæ, there being six or eight such ridges extending into each tooth.

In a few species, which for additional reasons to be adduced later are to be regarded as among the farthest advanced phylogenetically, a peculiar highly specialized type of scale has developed. The extremely brilliant luster of the white markings of *L. morrisella* and *ostensackenella* and *P. desmodiella* and of the bronzy purple metallic reflections on the thorax and base of the wings of *P. desmodiella* is produced by these scales. These white scales, one of which is illustrated by *Fig. 6*, are broader than the usual type, and the sides curve outward from the base. The outer edge of the scale, instead of being coarsely and acutely dentate as in

FIG. 6. White wing scale of *L. morrisella*.

the ordinary scales, is obtusely dentate or, sometimes, the teeth are entirely absent. The edge then appears scalloped, in a manner similar to the edge of a pecten. The depressions between the striæ, which appear rather broader and more widely separated than usual, are concave. The concavities between these striæ appear as if formed by a sloping out of the sides of the striæ. The assumption of a concave surface will explain the

brilliant and slightly opalescent luster of these scales; the various colors being produced by essentially the same processes as they are in a soap film. These scales contain no pigment whatever; the effects observed are due entirely to the effect of light passing through a medium of varying thickness. It may be noted here that in *L. robiniella*, a species very closely related to *L. morrisella*, this differentiation has not reached the same degree of perfection. The white scales are, however, broader and with fewer striæ than those of the more typical species. The metallic purple scales of the base of the wings and thorax of *P. desmodiella* are very similar to the white scales structurally but differ in that they contain a brownish pigment. Their metallic iridescence may undoubtedly be ascribed to the same agencies.



FIG. 5. Apical wing scale.

(c) COMPARATIVE STUDY OF THE ADULT MARKINGS.

The following study of the adult markings was instituted for the purpose of discovering whether, as was suggested earlier in the paper, the primitive

color pattern of the genus, or an approach to it, still exists among the modern species. The presence, in several species, of a number of almost straight or slightly modified transverse bands, separated from one another by unpigmented fasciæ, suggested the possibility that such a transversely banded arrangement of pigment areas, alternating with unpigmented fasciæ, was the primitive color pattern of the genus. This idea received some support from the fact that in *L. tiliacella*, whose pattern will be described in detail below, the bands in the apex of the wing are uniformly pale yellow, with no trace of darker scales. Bearing in mind the generally accepted fact that, phylogenetically, pale yellow is one of the oldest pigmental colors, some portions of the wing of *L. tiliacella* are probably still in the ancestral condition. In this species, seven distinct color areas can be made out, most of which are completely separated from one another by white (unpigmented) areas which lie over the origins or the tips of the nervures. As no species has been found to have a greater number of separate pigmented areas, and most of those which do not show a banded type of marking have fewer such areas, the conclusion was reached from the study of the adult markings that *the primitive color pattern consists of a series of seven transverse bands, separated from one another by unpigmented areas.*

The verification of this conclusion rests upon the studies of pupal development of the color pattern, which have also shown how the modifications in the color pattern, characterizing the different groups described below, have been brought about.

The evidence for the above conclusion as to the primitive color pattern, in so far as it is based upon adult characters, is given below. In this relatively brief survey of the adult markings of the numerous species comprising the genus *Lithocolletis* and its subgenera, the writer has been guided in the grouping of the species, as far as practicable at this stage of the presentation of the results of the research, by affinities determined through the discovery of the action of certain definite laws in bringing about changes in the shape and extent of the color areas. Occasionally, it has been found convenient to bring in arbitrary distinctions, used to separate the species systematically. This is true in the second group of species discussed; here the presence of a median fascia, while doubtless a character valuable to the taxonomist, is in no way an indication that the species are closely related to one another. Evolution has proceeded along the same line in the different species in respect to this one characteristic alone; the differentiation of the other markings has been brought about in such different ways as to indicate the early branching of this stem of the phylogenetic tree.

In the discussion of the individual species, the characters referred to are those developed through the action of general evolutionary tendencies. The various levels which such development has reached before coming to a standstill, mark the points where the different subgroups of species diverge from the main stems. Within these subgroups, there have been numerous differentiations, producing the actual species we now know. Such specific differences must be

minor ones, since the general plan of coloration has been already determined. Where a group of species has branched early from the main stem, the individual species within it will be found to be less closely related; the longer period of time allowed for differentiation within the group has given opportunity for greater divergence of the individuals composing it.

In general, no effort has been made to discuss the minute characters separating the species. Such characters and their processes of differentiation are more properly discussed later.

Leaving out of consideration for the present the species of the subgenera *Porphyroselu* and *Cremastobombycia*, the main branch of the genus may be divided, as has been mentioned earlier in this paper, into two natural divisions, sufficiently distinguished from one another by the type of larva and by the position with respect to the white fasciæ and streaks of the dark scales bordering them.

In the division whose larva in the later stages is of the normal cylindrical type, when a dark margin occurs on but one side of a white mark, it is present on the internal edge. In the majority of the species, this margin is the only one present; in some species, however, external margins have developed adjacent to some or all of the streaks. The external margin is, as a rule, considerably paler and less complete than the internal one; in a few cases, where both are equally well developed, other characteristics will leave no doubt of the division to which any species belongs. For convenience of reference, this division has been designated Division I. The species are illustrated on Plate III.

Several well-defined groups are recognizable. Some of these include a considerable number of species, showing close intergradations and indicating their origin from a common ancestor at a no very remote period. Other species seem to stand apart, showing no very clear affinities with any of the existing species.

One group, comprising *L. tiliacella* (Fig. 1, Pl. III; Text Fig. 7), *oregonensis*,¹ *affinis*,¹ *tritaniella* (Fig. 5), *ostensackenella* (Fig. 7) and *mariaella* (Fig. 8) as typical forms, and *fragilella* (Fig. 3) and *celtifoliella* (Fig. 4) as extreme deviations from the typical, is characterized by the presence of at least two complete white transverse fasciæ, the first crossing the wing at about the basal fourth, the second near the middle.

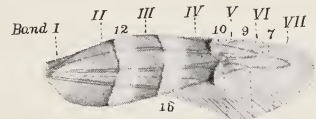


FIG. 7. Forewing of *L. tiliacella*.

In *tiliacella* (Fig. 7), the ground color is a very pale golden; a spot at the base of the dorsal margin is white; the two fasciæ are almost straight, the first but faintly dark margined. At three-fourths of the wing length, there are two white dark-margined spots, corresponding in position to a third fascia, very narrowly separated by pale golden scales which unite with a pale band of the ground color beyond. Then follows a fourth white fascia, separated from the apex of the wing by a few pale golden scales which mark the position of a band

¹ It was impossible to obtain figures of *L. oregonensis*, *affinis*, *occitanica* and *alni*.

of the ground color. Sometimes the apex of the wing is pure white; sometimes the extreme tip has a few golden scales. There are thus six white spots (four of these are the extremities of fasciæ) along the dorsal margin and five on the costal margin, separated from one another by ground color. These correspond in position with the points of origin or with the tips of the nervures. The positions of the white spots with respect to the nervures are as follows: the white streak at the base extends somewhat obliquely, lying over the point of origin of the tubular part of the upper median vein; the first fascia lies proximally over the tip of vein 12, distally over the origin of the tubular part of the upper median vein; the second fascia on the dorsal margin lies over the tip of vein 1b; the pair of white spots at three-fourths lie over the tips of veins 10 and 2 respectively; the white fascia beyond, over 9 and 5; the last white fascia lies over vein 7 on the costa. These white unpigmented areas are the interspaces between bands of ground color, seven in number, of which the first two are united on the costa.

In *L. oregonensis*, the same number of white interspaces are present with the exception of the white spot at the base of the dorsum, but the fasciæ are more bent. The ground color is a deeper golden, and, whereas in *tiliacella* the fasciæ beyond vein 10 are represented by a few pale yellow scales only, the ground color is distinct, and the fourth fascia is black margined. The extreme apex of the wing, which in *tiliacella* showed only a faint tinge of golden, contains a black apical spot. In *affinis*, *tritænianella* (Fig. 5), *ostensackenella* (Fig. 7) and *maricælla* (Fig. 8) there is a reduction in the number of white fasciæ and spots; the spots over veins 9 and 5 are wanting, and the ground color extends uninterruptedly from vein 10 to vein 7. In *ostensackenella*, the white streak enclosing the apex has become divided into a pair of opposite spots; the base of the wing is dark brown. In *affinis* and *tritænianella*, the white streak before the apex does not extend entirely across the wing. In *tritænianella*, the first white fascia is situated before the tip of vein 12. As it occupies the same position with respect to the origin of the upper median vein as the corresponding fascia in *tiliacella* (Fig. 7), it would seem that the origin of this vein is the factor determining the position of the first fascia. This conclusion is corroborated by identical observations on other species.

L. fragilella (Fig. 3) and *L. celtifoliella* (Fig. 4) are not closely related to the preceding members nor to one another. In both, the fasciæ are densely dusted internally with dark-tipped scales; in *fragilella*, the fasciæ are suffused with pale yellow; in *celtifoliella*, the fasciæ are acutely angled, and the oblique costal and dorsal arms reach the margins proximal to their usual position. As will be seen later, this displacement of the extremities of the first two fasciæ proximally is of common occurrence and has been one of the principal forces in the evolution of the species of this genus.

Desmodiella (Fig. 9), the single representative of the subgenus *Porphyrosela*, which structurally is in advance of *Lithocolletis*, has retained the banded

type of marking. There are two lustrous white fasciæ, dark margined on both sides, on a dark reddish brown ground color, showing a deep purple metallic luster at the base of the wing.

In another group of species, the median fascia only has been preserved, either in its primitive almost straight condition or has become angulated. Most of the species bear no close relationship to one another, and it would seem, therefore, that the group is merely an artificial one and that the characteristic of a median fascia is one which appears in several divergent lines of development. The species which may be included in this group for purposes of discussion are the following: *L. morrisella* (Fig. 48), *uhlerella* (Fig. 49), *lucetiella* (Fig. 51), *symphoricarpella* (Fig. 54), *gemmea* (Fig. 53), *martiella* (Fig. 52), *celtisella* (Fig. 56) and *apicinigrella* (Figs. 55a, 55b). *Robiniella* (Fig. 50) shows a very clear natural relationship with the first two mentioned species, and differs from them only by the separation of the median fascia into a pair of opposite costal and dorsal streaks,¹ and the obliteration of the first dorsal streak by dark scales.

Morrisella (Fig. 48), *uhlerella* (Fig. 49) and *robiniella* (Fig. 50) are a remarkably homogeneous triad of species; the figures will suffice to give a clear idea of their characteristics. In *lucetiella* (Fig. 51), the entire basal half of the wing is white, with the exception of a longitudinal streak from the base following the course of the upper median vein; the apical half of the wing closely resembles that of *tiliacella* (Fig. 7). In *symphoricarpella* (Fig. 54), the basal half of the wing is of the golden brown ground color; the white streaks over veins 9 and 5 are lacking. In *martiella* (Fig. 52) and *gemmea* (Fig. 53), there is a white basal streak;² in *gemmea* a white spot on the dorsal margin occupies a position nearly corresponding to the extremity of the first fascia. In these two species, as in *morrisella*, *uhlerella* and *robiniella*, a group of small scales in the apex forms the black apical dot. *Celtisella* (Fig. 56) and *apicinigrella* (Figs. 55a, 55b) are characterized by the presence of an acutely angled fascia and a median white basal streak. In *celtisella*, the dorsal margin is also white from the base to the fascia. *Apicinigrella* is an extremely variable species; sometimes the fascia is broken in the middle; an extreme aberrational form is represented by Fig. 55b.

Basistrigella (Fig. 57), although a somewhat isolated species, is perhaps most closely related to *celtisella* (Fig. 56) and *apicinigrella* (Figs. 55a, 55b) of the above group. The median pair of streaks are of equal width throughout and each is extended at its extremity along the margin to the base.

Bataviella (Fig. 58) stands entirely apart from any of the species of the American fauna; there are, however, several closely related species in the European fauna. The white spot which was present at the base of the dorsal margin in *tiliacella* and did not reach the costa, is here often extended entirely

¹ The terms "costal streak" and "dorsal streak" are used to designate the white and usually triangular spots situated on the costa and dorsum respectively.

² The "basal streak" is the white longitudinal line beginning at the base of the dorsum and extending along the middle of the wing for about one-third its length.

across the wing thus separating a basal patch of dark scales from the band of similar scales beyond it. In this species, therefore, the number of distinct patches or bands distinguishable along the costa is seven, separated more or less completely from one another by white interspaces.

The remainder of the species, and by far the most numerous, have been included in one large group, because all can be traced to a common origin and all are manifestations of a similar tendency in development. All are characterized by the presence of pairs of opposite curved, oblique costal and dorsal streaks, widest on the margins and tapering in the middle of the wing to pointed apices. There are a number of well-defined subgroups, due to the halting of individuals at different stages in the general process of evolution and the differentiation of a number of species from each of these.

Standing at the foot of the group and somewhat apart from the other species, is *auronitens* (Fig. 10). In it, there are three dorsal streaks before the tornus,¹ but little oblique and not displaced proximally from their normal position with respect to the nervures.

Argentinotella (Fig. 11), *occitanica* and *leucothorax* (Fig. 13) are also characterized by the presence of three streaks on the dorsum before the tornus. These are decidedly oblique, especially in *leucothorax*, in which there is also a well-defined apical spot. In *occitanica*, the first, fourth and fifth costal streaks present in *argentinotella* are wanting.

In *fitchella* (Fig. 14), there are but two dorsal streaks before the tornus; the first is unusually large, suggesting from its position the possibility of its formation from two white streaks. That this has occurred and the processes bringing it about will be discussed later.

Salicifoliella (Fig. 15) and *tremuloidiella* (Fig. 16) are not closely related to any of the large subgroup of species soon to be discussed. These two isolated species are the result of differentiation and advancement along other lines, when there has been a cessation, at a lower level, of the common course of evolution, which if continued, culminates in such forms as *hageni* (Fig. 17) and later, in the large subgroup of species of which *cratægella* (Fig. 36) and *obscuricostella* (Fig. 25) are typical representatives. Because of this, their markings will be better understood when the laws governing their transformation have become apparent.

Insignis (Fig. 20), *hageni* (Fig. 17) and *arbutusella* (Fig. 18) are properly grouped together. In another variety of *insignis*, the white extends from the basal streak across the wing to the dorsum, forming a quadrate white patch similar to that of *hageni*. These three species are likewise differentiations from an offshoot of the main stem, although at a higher level than the two preceding species.

We now come to the large subgroup of species characterized by two oblique

¹ The three margins of the wing are the costa or upper margin, the termen or outer margin and the dorsum or inner margin. The junction of the costa and termen is the apex of the wing; the junction of the termen and dorsum is the tornus. In this group, where there is no defined termen, the tornus is the place where the line of scales in the cilia meets the dorsal margin.

streaks on the dorsum, the first usually very oblique, the second, which is placed at the tornus, often nearly perpendicular, and four costal streaks (rarely five as in *populiella* and *rileyella*). These are *populiella* (Fig. 27), *diaphanella* (Fig. 28), *salicivorella* (Fig. 29), *deceptusella* (Fig. 30), *alnicolella* (Fig. 32), *alni*, *incanella* (Fig. 34), *scudderella* (Fig. 35), *ledella* (Fig. 33), *malimalifoliella* (Fig. 37), *crataegella* (Fig. 36) and *propinquinella* (Fig. 38), in which the black scales in the apex are not massed to form a circular apical dot; and *caryæalbella* (Fig. 21), *rileyella* (Fig. 22), *ostryæfoliella* (Fig. 23), *olivæformis* (Fig. 24), *obscuricostella* (Fig. 25), *kearfottella* (Fig. 26), *obsoleta* (Fig. 41), *sexnotella* (Fig. 39) and *æriferella* (Fig. 40), in which a number of small black scales in the apex are grouped into an almost circular, definitely outlined, apical spot. In *obsoleta* (Fig. 41), this spot is very ill-defined, as are all the other markings. With the exception of the three last mentioned species, a white median basal streak extends to about one-third of the wing length. This streak may be margined above and sometimes around its tip with dark scales. In some of the species, there is, on the dorsal margin, a small white spot, often extended almost to the base of the wing and with its outer edge about midway between the base of the wing and the first dorsal streak. In a few cases (*e. g.*, *incanella* (Fig. 34)), this spot is indistinctly margined on its inner side by a short oblique line of darker scales. In *obsoleta* (Fig. 41), *sexnotella* (Fig. 39) and *æriferella* (Fig. 40), the entire basal portion of the wing is without markings, the ground color extending uniformly over it.

Lastly, there is that subgroup of species in which there is but one margined dorsal streak and that one is situated at the tornus; the basal portion of the wing is, to a great extent, shining white, and any colored markings present are longitudinal. These are *trinotella* (Fig. 47), *quercialbella* (Fig. 46), *clemensella* (Fig. 45), *lucidicostella* (Fig. 44) and *argentifimbriella* (Fig. 43). Phylogenetically considered, *albanotella* (Fig. 42) should be included here, as representing an earlier stage in the process resulting in the production of these five species. In this species, a first dorsal streak is defined by an incomplete margin not reaching the dorsum.

In Division II of the genus, illustrated on Plate IV, where the modified flat type of larva persists through six larval instars, the chief aggregation of dark scales is on the outer side of the white streaks and fasciæ. Where an additional margin occurs on the inner side of the white markings, the outer one has broadened considerably and is often prolonged at the angle of a fascia as a dense aggregation of dark tipped scales. There seems to be less tendency in this group toward the concentration of dark scales in the apex over a definitely outlined area; the tendency is rather for all the scales to become dark tipped, producing an evenly dusted effect. As in Division I, several groups of species are recognizable.

In one group, there is a tendency to preserve, either straight or angulated, two white fasciæ, the first crossing the wing at the basal fourth, the second at the middle. In *obstrictella* (Fig. 64), these fasciæ are almost perpendicular and straight; the pair of white streaks beyond often form a third fascia. In

tubiferella (Fig. 65), *aceriella* (Fig. 66) and *hamameliella* (Fig. 67), these fasciæ are straight and but little oblique. In *tubiferella* (Fig. 65), they are the only white markings, except sometimes a very small white dot near the apex. In *aceriella* (Fig. 66) and *hamameliella* (Fig. 67), there are, in addition, an oblique white streak at the base of the dorsum, a longer oblique dorsal streak at the tornus and a small white streak opposite it on the costa. *Ostryarella* (Fig. 68), *corylisella* (Fig. 69), *æsculisella* (Fig. 70) and *guttifinitella* (Fig. 71) constitute a closely related series, separated from one another by small differentiations. In these species, the two fasciæ are bent outwardly below the costa, scarcely enough to be called angulated. In *guttifinitella*, the pale streak at the base of the dorsum is almost or sometimes entirely wanting. In *lentella* (Fig. 73) and *caryæfoliella* (Fig. 72), the fasciæ are distinctly angulated.

In *cinninatiella* (Fig. 75), *macrocarpella* (Fig. 74), *saccharella* (Fig. 76), *hamadryadella* (Fig. 77), *umbellulariæ* (Fig. 78) and *agrifoliella* (Fig. 79), at least one of the two white fasciæ has become acutely angulated. In *hamadryadella* (Fig. 77) and *umbellulariæ* (Fig. 78), the white fascia at the base is preserved to the costa, although in *umbellulariæ*, it is almost separated into two parts. In *agrifoliella* (Fig. 79), the position of this fascia is indicated by two patches of dark scales which would form its external margin. In *hamadryadella* (Fig. 77), very complete internal margins to the white fasciæ have developed; the ground color has, however, shrunk away toward the base, so that the line of dark scales extends through the middle of a broad white band. In *cinninatiella* (Fig. 75) and *macrocarpella* (Fig. 74), the two fasciæ are uniformly angulated; the white patch at the base does not reach the costa. The costal arm of the first fascia of *saccharella* (Fig. 76) is wanting, its dorsal arm is very oblique and confluent with the oblique basal streak.

A group of species comprising *fletcherella* (Fig. 80), *arcuella* (Fig. 81), *betulivora* (Fig. 82), *australisella* (Fig. 83), *bethunella* (Fig. 84), *chambersella* (Fig. 85), *cervina* (Fig. 86), *platanoidiella* (Fig. 87), *castaneæella* (Fig. 88) and *fasciella* (Fig. 89) retains but the single median fascia, sometimes almost divided at its angle. A pair of opposite oblique streaks represent the former complete fascia at the basal fourth of the wing in the five first mentioned species of this group; in the remaining five, the costal streak only is present. In *castaneæella* (Fig. 88) and *fasciella* (Fig. 89), there has been an extensive progressive diminution in the white markings; the median fascia is the only white marking remaining in *fasciella*.

In *gaultheriella* (Fig. 91) and *nemoris* (Fig. 90), there is no median fascia; instead of it a pair of costal and dorsal streaks. In *nemoris*, the first pair of streaks meet, forming a fascia; in *gaultheriella*, they are separate.

Lastly, there is that group of four species, in which a white longitudinal streak extends from the base along the dorsal margin, reaching to or beyond the middle. These are *mediodorsella* (Fig. 92), *quercivorella* (Fig. 93), *ulmella* (Fig. 95) and *conglomeratella* (Fig. 94). In the two former, this streak stops abruptly at the middle of the dorsal margin; in *mediodorsella* (Fig. 92), it connects with

the dorsal arm of an angulated fascia. In *ulmella* (Fig. 95) and *conglomeratella* (Fig. 94), the white streak extends almost to the tornus, where it connects with a dorsal streak running obliquely into the apex.

A rather noteworthy feature common to both divisions of the genus is this: the third white fascia or the third pair of streaks, whose extremities are placed over the tips of veins 2 and 10, are never displaced from their normal position, and only in rare instances are they much oblique. These instances are almost entirely confined to Division II. In such case, the impression of length and obliquity is gained through the fact that the more apical portion of this streak is homologous with the white streak over vein 5. The greatest changes have taken place in the positions of the first two pair of streaks, resulting in their displacement toward the base.

In either of the two divisions of the genus, the greatest number of more or less distinct bands of ground color has been seven. The first of these crosses the base of the wing and is usually confluent with the second in the costal half of the wing. The position of the white unpigmented areas separating these bands of ground color appears to be determined by the points of origin or by the tips of the longitudinal nervures. The question to be decided is whether such a banded arrangement of pigment areas represents the primitive type of coloration, and if so, how has evolution acted in bringing into existence the present great complex of species.

A group of species (Figs. 59a, 59b, 60, 61, 62, 63) more primitive in generic structure, namely, *Cremastobombycia*, shows a type of coloration strikingly similar to that of some of the species of the "flat-larval group." An examination of this group discloses the fact that nowhere are there more than four costal white streaks as compared with five or six in some of the species of the more recent branches of the genus. Apparently, then, because of the fewer separate bands of ground color present in species of this group, the primitive type of marking is not to be sought for among the species of the ancestral group.

The observations that have been made point to the conclusion that the primitive type of coloration is made up of seven distinct transverse bands. The results of the investigations upon the development of color in the pupal wings, now to be presented, confirm this view and, in addition, furnish evidence of the means by which transformation of the bands into the various types of color pattern has been accomplished.

(d) ONTOGENETIC DEVELOPMENT OF THE COLOR PATTERN.

1. *Historical.*

Tower ('06) has summarized the general results of researches upon the development of colors in pupal wings as follows:

"The studies upon the origin of color in the wings of Lepidoptera have shown that there is a regular order of development, not only of colors but also of the areas in which spots and stripes appear. The wings, which are colorless

at first, become opaque, yellowish or light drab, beginning first near the base of the wing and spreading distalward. Soon spots, stripes and adult markings appear, at first proximad, then more and more distad, then between the nervules and, last of all, upon the nervules. First, the purely pigmental or chemical colors develop, and these are followed by the chemico-physical."

The principal researches have been those by Schäffer ('89), Van Bemmelen ('89), Urech ('91), Haase ('93), Mayer ('96) and most recently by von Linden ('98, '02). The principal work of the first three authors was upon *Vanessa* and *Pyrameis*. Van Bemmelen ('89) has shown that the first color to appear in *Pyrameis cardui* is a pale brownish yellow which deepens to the reddish brown ground color; upon this ground color, the black spots appear. The development of the color in *Vanessa urticae* follows very much the same sequence, as pointed out by both Van Bemmelen and Urech. Urech ('91) has shown that in *Vanessa io*, the adult spots and colors appear directly upon the primitive white of the pupal wing; that is, the yellow appears over a restricted area of the wing; following this, a reddish tinge appears, which, over another portion of the wing, gradually deepens to the reddish brown ground color. Later, the adult black spots develop directly upon the primitive white wing; some at least of the white spots of the adult represent the primitive white of the pupal wing. In Van Bemmelen's opinion, a considerable amount of modification takes place in the wings after the first appearance of color, so that the adult design may differ considerably from that first laid down. Urech's ('91) view is directly opposed to this; according to him, the different color areas are definitely laid down from the beginning and are therefore older phylogenetically than the particular colors of the adult wing. He therefore regards color as the important factor in determining phylogenetic position—"die Farbe ist das Primäre, die Zeichnung das Secundäre."

Haase ('93) worked upon several species of *Papilio* and found that the wings are transparent or colorless, later becoming whitish; this white then gives way to a yellowish ground color upon which the adult colors begin to appear, undergoing considerable development before reaching their definitive adult condition.

Mayer ('96) traces the development of the scales from modified hypodermis cells, the "formative cells of the scales," from their first appearance as blunt outgrowths from these cells until they are fully formed and pigmented. In addition to confirming the conclusions of previous investigators as to the sequence in the appearance of colors, Mayer has shown that "the transparent condition of the wings corresponds to the period before the scales are formed and to the time when they are still completely full of protoplasm. The white condition is caused by the withdrawal of the protoplasm from the scales, leaving them as little hollow bags filled with air. In this condition, they diffract the light and appear pure white.

"After the protoplasm has completely withdrawn from the scales, the

'blood' or hæmolymph of the pupa enters them, and soon after this, the wing becomes of a uniform dull yellow or light drab color. This color is due to the fact that soon after the hæmolymph has entered the scales, it changes to a dull ochre-yellow and finally to a drab color. The same change takes place in hæmolymph which has been removed from the pupa and exposed to the air. The mature colors are due to chemical changes in the hæmolymph itself. They first appear in places *between* the nervures, never upon the nervures themselves. The last places to acquire the mature coloration are the outer and costal edges of the wings and the nervures. . . .

"Dull ochre-yellow and drabs are, phylogenetically speaking, the oldest pigmental colors in the Lepidoptera, for these are the colors that are assumed by the hæmolymph upon mere exposure to air. The more brilliant pigmental colors, such as bright yellows, reds, greens, etc., are derived by more complex chemical processes. We find that dull ochre-yellows and drabs are at the present day the prevalent colors among the less differentiated nocturnal moths. The diurnal forms of Lepidoptera have almost a monopoly of the brilliant colorations, but even in these diurnal forms, one finds that dull yellow or drab colors are still quite common upon those parts of their wings that are hidden from view."

The most recent researches upon the subject of development of color in the pupal wings of Lepidoptera are those of von Linden ('98, '02). The results of her investigations are embodied in two papers, the first being practically included in the second. Her observations lead to the conclusion that the adult color pattern develops from a number of separate transverse bands which dispose themselves upon a uniform ground color in a manner characteristic of each species. A distinction is thus made between ground color and that forming the color pattern. These transverse bands (longitudinal according to Eimer's view) occupy definite positions upon the wing determined by the course of the nervures and tracheæ. This is the condition found among Papilios, Vanessas, Sphingids, the higher Bombycids and even among some of the Geometrids. These larger bands are formed by the broadening out and fusion of narrower bands ("bandelettes primaires") preserved only among more primitive forms. On the one hand, the bands may fuse to form a uniform color; on the other, they may break up into a series of spots, which become smaller as the ground color encroaches upon them. The hindwing is arrested at a point less advanced than the forewing; this, combined with the greater tendency toward fusion of the bands which is in fact due to the modified form of the hindwing, creates the erroneous impression that the hindwing is more advanced than the forewing.

The author claims that her results support the laws which Eimer has promulgated for species differentiation based upon a study of adult coloration:

"Il est donc évident que les lois que Eimer a trouvées en étudiant la phylogénèse du dessin des Lépidoptères peuvent être admises point pour point pour l'ontogénèse."

"Mes recherches prouvent donc que le dessin des Papillons ne paraît pas soudainement, . . . que les phases que ce dessin parcourt pendant son développe-

ment ontogénétique, sont analogues aux phases que le dessin de l'espèce du Papillon a dû parcourir pendant son développement phylogénétique, que le loi qui gouverne la biogenèse est aussi confirmée par ce procédé, qui s'accomplit pendant la métamorphose de l'insecte, et qu'en fin les théories de Eimer sont solidement fondées, quand il dit que chaque animal ne peut varier que dans peu de directions déterminées par les influences du dehors et par sa propre constitution, et que l'espèce se forme par génépistase."

Recapitulation is, however, only partial and confined to primitive forms:

"Les phénomènes de la phylogénèse se produisent le plus clairement dans le développement du dessin chez les formes *les plus primitives*. Chez les groupes *les plus avancés*, ces phénomènes sont masqués par l'intervention de la tachy-génèse qui montre sa plus grande influence dans le développement des ailes inférieures."

With regard to the succession of colors upon the wing, the same author finds that it is only in the primitive forms that the scales forming the dark markings pass through the intermediate shades of yellow to reach their final gray or black condition; in the higher forms, they remain uncolored until the scales forming the ground color reach their full development, later passing directly from the colorless stage into gray or black. The color appears first at the tip of the scales, spreading gradually to the base. Scales which are destined to acquire their pigment later are not fully formed when the scales of the ground color attain the adult form and color. Therefore, color may be taken as a measure of the degree of development of a scale.

2. Methods.

In the study of the development of color in the wings of *Lithocolletis*, specimens of the summer generations were used for observation. No overwintering pupæ have been observed. In the summer generations, the average duration of the pupal state is about a week; it may be as short as four or five days.

The chrysalids were removed from the mines shortly after pupation and kept under careful observation. For some time, no change in the brown color of the pupa is to be observed, then two faintly darker brown spots, corresponding in position with the eyes of the imago, become visible through the pupal envelope. These spots rapidly turn black, and very shortly after, the wings, which up to this time have appeared transparent through their thin chitinous envelope, begin to lose their transparency. This marks the beginning of the white stage. A day or two later, the yellow colors begin to appear upon the wing. The chief difficulty in the study lies in securing a suitable series of these earliest stages, as the colors are very faint at this period, and numerous dissections are often required before the necessary material can be obtained. In later stages, the markings are visible through the pupal envelope, and a choice of specimens can be made with relative accuracy.

The dissections were made in .6 per cent NaCl solution under a simple

dissecting microscope of moderate power by means of fine needles set in matchsticks. One needle is inserted through the abdomen and held rigid; another through the middle of the upper side of the thorax. The second needle is now drawn forward, tearing apart the pupal envelope and carrying with it the anterior part of the thorax with wings attached. The structure of the pupa with separate envelopes for wings and legs in the lower Microlepidoptera renders this method of procedure highly successful. The thorax may now be torn apart, allowing the wings to float out flat. With a little experience, it is possible to remove the wings in this manner without the displacement of either scales or cilia. The wings thus removed from the pupa vary in length from 1.5 to 2 mm., being, therefore, about one-half the length of the imaginal wings.

The wings were examined with a simple lens to determine the general extent of the color areas. For the more accurate observation of the positions and limits of pigmented areas and individual scales pigmented, I have used a compound microscope, 16 mm. objective, 4x eyepiece, giving a magnification of 60 diameters. The observations were made almost entirely by reflected light and under a cover glass. In the early stages, where the colors are very faint, I have found black paper, as suggested by von Linden, very useful for a background. Somewhat later, a pure white background is advantageous in the detection of the first appearance of grayish tints.

All of the wings were examined in .6 per cent NaCl solution, shortly after removal from the pupa. Observations made thus are vastly more satisfactory than when permanent mounts are employed. A number of the wings were, however, transferred to absolute alcohol between pieces of glass to prevent curling, and after about an hour embedded in Venetian turpentine made as follows:

Commercial Venice turpentine is mixed in a tall cylinder glass with an equal volume of 95 per cent alcohol. The mixture is allowed to stand in a warm place for three or four weeks and then decanted.

The mounting medium thus prepared is thin enough to flow easily and not displace the delicate cilia. However, the attendant darkening of the colors is a disadvantage in comparing with adult specimens.

I have found it possible to preserve all except the earliest stages without the use of a mounting fluid, if the slide containing the wing under a cover glass is immersed in absolute alcohol for a short period. Later the cover glass may be closely appressed and fastened down around its edges.

Both forewings in each specimen were examined; the two sets of observations thus serving as a check on one another. In the following descriptions, reference is made to the forewings only. The hindwings are practically unicolorous, usually paler than the forewings, and reach their final development somewhat in advance of the forewings. Their development yields no new facts, merely confirming the results of earlier investigators upon the sequence of colors.

3. Observations.

Two factors were taken into consideration in determining the choice of species to be studied, namely, the general type of adult marking and the presence or absence of certain characters such as an apical spot or dark marginings adjacent to white streaks or fasciæ. The object of the research is twofold: (1) to determine, if possible, the primitive or fundamental color pattern and its mode of transformation into the adult pattern and (2) to determine the relative time of appearance and manner of development of the various dark markings, the characters referred to above.

The evidence furnished by the development of color in the pupal wings taken in conjunction with a comparative study of the adult markings has convinced me that the primitive color pattern is composed of a series of uniformly colored pale yellow bands, seven in number, placed transversely on the wing and separated from one another by white fasciæ (unpigmented areas) (*Fig. 8*). These bands are typically straight and, with the exception of the first, cross the wing almost perpendicular to the margins. The bands, when present in their primitive condition, have certain defined positions. Their hypothetical typical positions are illustrated by *Fig. 8*. In what follows, it will be noticed that there is a definite relation of bands to veins. Band I occupies the extreme base of the wing, beginning at the base of the dorsum and broadening on the costa; the white streak which separates it from Band II passes obliquely from the base of the dorsum toward the costa, lying over the point of origin of the tubular portion of the lower median vein. Band II crosses the wing on the basal side of the tip of vein 12; the position of the white fascia which separates it from Band III seems to be determined rather by the point of origin of the tubular portion of the upper median vein than by the tip of vein 12, as this vein often extends considerably beyond the origin of the upper median vein without causing a corresponding broadening distally of the second band. It sometimes happens that vein 12 is unusually short, and then the white fascia lies over its tip and over the origin of the upper median vein. On the costa, the inner border of Band III lies just beyond the origin of the upper median vein, and on the dorsum, the outer border extends almost to the tip of vein 1b. Band IV crosses beyond the tip of vein 1b and lies over the bases of veins 10 and 2, its outer border being just within the tips of veins 10 and 2. Band V on the costa is placed between veins 10 and 9, on the termen between veins 2 and 5 and lies over the transverse vein. Band VI is placed between veins 9 and 7 on the costa and beyond vein 5 on the termen. Band VII crosses the apex of the wing. Thus it will be seen that the position of the bands is largely determined by the position of the longitudinal nervures, the tips of the veins marking the extremities of the unpigmented fasciæ separating the bands. In no case in the adult has this pattern

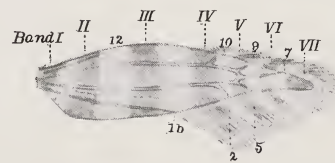


FIG. 8. Hypothetical primitive color pattern of the forewing of *Lithocolletis*.

been preserved in its original primitive condition as seven distinct transverse bands; fusions either partial or entire have taken place between two or more adjacent bands. Displacements have also occurred, due to a shrinking away of color from one side of a white interspace and its extension over the white on the other side. Finally, some of the bands may have shrunk away almost entirely.

The following is a list of the species in which the development of the pattern has been traced from the first appearance of color to the adult markings:

<i>Lithocolletis tiliacella</i> Cham.	} Species in which two or more of the bands have been preserved almost in their primitive condition as respects position and shape.
<i>Lithocolletis tritænianella</i> Cham.	
<i>Lithocolletis cratægella</i> Clem.	} Species in which changes in shape or position or both and more or less complete fusions of some of the bands have taken place and certain differentiations and specializations have appeared, such as the development of black scales at places other than those directly contiguous to the white interspaces between the bands.
<i>Lithocolletis ostryæfoliella</i> Clem.	
<i>Lithocolletis lucidicostella</i> Clem.	
<i>Lithocolletis morrisella</i> Fitch	
<i>Lithocolletis hamadryadella</i> Clem.	
<i>Lithocolletis bethunella</i> Cham.	
<i>Lithocolletis ulmella</i> Cham.	
<i>Lithocolletis æsculisella</i> Cham.	
<i>Cremastobombycia ignota</i> F. and B.	

In the following species, the development of the pattern was observed only in part for the purpose of comparing the development of certain characters in these species with that of similar characters in related species, or with a view of determining the relative time of appearance of certain characters:

Lithocolletis hageni F. and B.
Lithocolletis robiniella Clem.
Lithocolletis caryæfoliella Clem.
Cremastobombycia solidaginis F. and B.

In all of the species studied, the wings are at first transparent and glassy in appearance, corresponding to the period, as observed by Mayer ('96), before the protoplasm has been retracted from the scales. Following this is the so-called white stage, in which the wings appear by reflected light almost pure white and by transmitted light pale buffish, due to the hæmolymph contained within them. The scales are at this period colorless and transparent, containing only air. The white stage lasts from one to two days, giving way to a pale yellow over certain defined areas, as the hæmolymph enters the scales and the pigment begins to form. This yellow color may be preserved throughout pupal development almost as originally laid down, or it may go through a process of transformation before reaching the adult condition. In either event, it gradually deepens in tint and constitutes the ground color upon which the dark streaks (margins)

and spots are to appear. The development of the pattern takes place very rapidly during the last part of the pupal state. The time intervening between the first appearance of a tinge of yellow on the wings and the emergence of the imago is largely dependent upon temperature and is often less than twenty-four hours. Development takes place more rapidly in day time than at night and is strikingly retarded during cloudy weather.

Lithocolletis tiliacella Cham.

In the first specimen examined, the wings were removed from the pupa at a very early stage of development. The yellow color is scarcely differentiated from the clear buffish white wing (*Fig. 9*). The only bands which can be distinguished are II, III and IV. Band II crosses the wing just before the tip of vein 12, thus occupying its primitive and typical position. It is the palest and least defined of any of the three bands present. Its outer edge is definitely defined, but its inner edge fades into the clear basal part of the wing, the color being extended farthest toward the base just within the costal and dorsal margins. Band III has also preserved its primitive position and form. It is somewhat darker than II, but uniformly colored throughout its breadth, the outer edge not darkened. Its width is scarcely greater than that of the clear band preceding it. Band IV is the most deeply colored as well as the broadest of the three bands; it is of the same breadth as in the adult. Even at this early stage it is prolonged outwardly almost to the end of the cell. The entire apical part of the wing and cilia are of the clear whitish color, there being no indication whatever of bands.



FIG. 9. Early stage in the development of color in the wing of *L. tiliacella*.

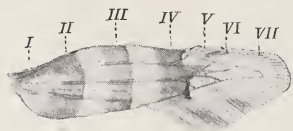


FIG. 10. Later stage in the development of color in the wing of *L. tiliacella*.

The wing in the next stage examined shows considerable advance over the stage just described (*Fig. 10*). There has been a decided deepening of color, and the adult pattern has been laid down, with the possible exception of Bands VI and VII, which have not as yet been clearly differentiated as bands although there is a faint yellow tinge in a few of the scales in the apical portion of the wing. These bands are usually indistinct and sometimes absent even in the adult. Band I is united with Band II along the costa; this condition was apparently not produced by the independent origin of Band I and its later fusion with II but by a uniform and gradual deepening of the wing below the costa. The outer edge of Band II is now somewhat bent outward in the middle, and the scales in the middle of the outer edge are beginning to deepen in color, thus foreshadowing the appearance of the dark margin, but there is as yet no *brown* pigment in the scales. Band III is also somewhat bent outwardly as in the adult, and its dark margin is present on the costa and dorsum only, the costal margin being much less distinct than the dorsal; neither extends more than a

short distance onto the wing proper. The middle of Band IV is faintly connected with a pale band beyond, which represents Band V. Its margins have reached more nearly their adult condition than any other of the wing markings. The margin on the dorsal half is almost as greatly developed as in the adult; that on the costal half is represented only by a few black scales.

The next stage studied shows no further change in the shape or extent of any of the bands, the changes which have taken place being confined to continuation of processes already begun, namely, the deepening of the outer edge of Band II, thus forming the internal margin of the first white fascia in the adult, the approximation of the costal and dorsal parts of the margin of Band III, so that they are now but little separated, and their darkening to the adult color, the advance of the margins of Band IV to their adult condition, the deepening of Band V so that it now appears quite distinct and as in the adult.

This is the only species studied which shows any distinction between the bands in regard to their relative time of appearance. Bands II, III and IV are the first to appear, and in the youngest specimen examined, Band IV was decidedly in advance of the other two as shown by its deeper color and by its extension outwardly in the middle. It is, therefore, probably safe to assume that Band IV is in this species, the earliest to appear ontogenetically. As will be shown later, *L. tiliacella* has probably in many respects conserved more closely than any other of the now existing species the primitive type of color pattern, and hence the sequence observed in the appearance of the bands in the ontogeny may also be true for the phylogeny.

Lithocolletis tritænianella Cham.

At the earliest stage at which it is possible to discern any indication of marking, five very pale yellow bands are visible upon the wing (*Fig. 11*). These

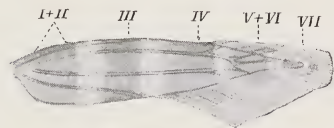


FIG. 11. Early stage in the development of color in the wing of *L. tritænianella*.

are uniformly colored and straight and are placed transversely upon the wing, showing no signs of fusion with one another. The first of these is, in fact, I + II, as shown by the faintly paler streak extending into it from the base of the dorsum. The second, Band III, occupies its usual position, but in this case the position of the white fascia separating it from II is wholly determined by the point of origin of the upper median vein, as vein 12 extends for a considerable distance into Band III. The third, Band IV, is normal in position and shape. That the fourth band is in reality composed of Bands V and VI is shown by its origin just beyond the tips of veins 10 and 2 and by its extension distally over the tips of 9 and 5 which in the primitive color pattern mark the position of the white fascia separating Bands V and VI. Band VII crosses the apex of the wing. The white interspaces between Bands II and III and between III and IV are of about the same width as in the adult, but that between IV and V + VI is considerably wider and shows no indication of the angulation which

is present in the adult; that is, Band IV has not yet begun to extend outwardly through the cell. The space separating V + VI from VII is at this stage about one-half the width of V + VI and extends entirely across the wing, thus differing strikingly from the condition found in the adult.

The development for some time consists merely in a uniform darkening of the ground color as first laid down without any change in the extent of the bands. At a somewhat later stage, simultaneously with the darkening of the ground color into the adult shade, changes in shape and more complete fusions of some of the bands occur. As soon as the adult color has been attained, the dark margins begin to develop. A specimen examined at this period shows that while no change has taken place in the form or extent of Bands I + II and III, Band IV has become outwardly angulated as in the adult, thus narrowing, especially in the middle of the wing, the white fascia separating it from V + VI. On the dorsal margin, Bands V, VI and VII are completely fused, the small white costal streak before the apex alone remaining to mark the position of the white fascia between V + VI and VII. The scales along the outer edges of Bands II and III are beginning to show faintly brownish tips, this color being about evenly distributed along the entire edge of Band II; in Band III, the color extends farther toward the bases of the scales in the middle of the wing. The scales of the dorsal half of the outer edge of Band IV are dark reddish brown, almost as in the adult, but on the costal half of the wing, there is only a very slight deepening of the yellow color, the margin here being considerably paler than the margins of Bands II and III. There is a very slight deepening of scales on the outer border of Band V + VI, adjacent to the white streak before the apex. The dusting in the apex is dense, the color being darker and more blackish than the outer margin of Band IV, and extends from the white streak well around the apex and along the dorsal margin almost to vein 5. This dusting is considerably greater in extent even in this stage than that of the overwintering forms in any stage.

***Lithocolletis cratægella* Clem.**

This species belongs to that large group in which the imago is characterized by the presence of pairs of opposite white costal and dorsal streaks; that is, all of the original primitive bands have fused at least along the middle of the wing. *L. cratægella* (Fig. 36, Pl. III) possesses in addition a margined basal streak, external as well as internal margins to the white streaks (*i. e.*, the dark scales developed on both sides of the primitive bands and not only on the outer side, as in the two preceding species), a streak of dark scales along the middle of the wing, a patch of black scales in the apex and the blue iridescence of the scales in the cilia. The study of the development of the wings in this form should therefore throw light upon the origin and mode of development of the above characters and indicate their relative time of appearance.

In the earliest stage examined (*Fig. 12*), at a period when the markings are

pale yellowish and but little differentiated from the colorless wing, the pattern strikingly resembles that of the adult insect. The white basal streak is distinctly outlined, beginning at the base of the dorsum, where it seems to be homologous

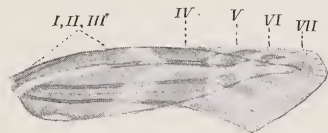


FIG. 12. Early stage in the development of color in the wing of *L. crataegella*.

with the white streak separating Bands I and II, beyond this lying over a trachea which extends through the cell just above the middle; its tip seems to coincide with some portion of the white fascia separating Bands II and III. The white patch near the base of the dorsum is identical with that in the adult and with the apex of the basal streak seems to constitute the last vestige of the white fascia separating Bands II and III. On the dorsal margin, the outer edge of Band III has shrunk away toward the base, and at the same time, there has been a compensating extension of Band IV toward the base, resulting in a displacement of the white streak, so that instead of being over vein 1*b*, it is basal to it, and vein 1*b* reaches the margin well within Band IV. The first pair of streaks are already separated by a narrow line, which is not nearly as broad internally as in the imago. At this stage, the costal white streak is not much narrower on the margin than the dorsal. Bands V, VI and VII are situated normally, except that V on the dorsum extends a little basally over the tip of vein 2. These bands, while quite distinct on the margins and in the cilia, seem to fade away in the middle of the wing. The entire middle of the wing, from the tip of the first dorsal white streak almost to the extreme tip of the wing, remains colorless, so that it is not possible to distinguish the bands from the interspaces separating them. A comparison with the adult shows that this area coincides with that to be occupied by the dark streak of scales through the middle and by the apical patch of black scales.

In a specimen somewhat more advanced, there has been a slight deepening of color, but by no means, even in the golden color, has the adult shade been attained. The color is still yellow, with no tinge of brown, unless the slight darkening of the dorsal side of Band IV, especially toward the second white streak, may be regarded as a foreshadowing of that color. The middle of the wing from the tip of the first dorsal streak almost to the apex (except for the grayish black scales to be noted below) still retains its whitish appearance. Just before the apex and beginning just under the tip of vein 7, and extending for a short distance along the underside of 7, are a number of grayish black scales. These appeared first beneath the tip of 7 and were gradually extended toward the base. The patch is broadest toward the apex, where it reaches almost across the wing. The inner edges of the first pair of streaks are more curved than in the preceding specimen as a result of the broadening internally of the yellow line separating them. The scales attached around the apex are yellow and extend in an unbroken line to the second dorsal streak, that is, Bands V, VI and VII have united along the termen. However, the scales whose apices project beyond these and which are destined to constitute the iridescent blue line in the cilia still remain pure white.

A specimen at a somewhat later stage (*Fig. 13*) shows a little more of the orange brown tint, but the color is nowhere as deep as in the adult. The formerly colorless area in the middle of the wing is still distinctly set apart from the rest of the wing but has become narrower and is beginning to acquire a faintly yellowish tinge. The white streaks are now definitely blocked out due to the curving in of the yellow color; they are, however, still connected with the whitish middle portion of the wing. The patch of blackish scales near the apex has increased in extent and depth of color until its identity with the patch of *black* scales in the apex of the adult wing is clearly established. It has now reached its adult condition, and no further change takes place. The early origin and differentiation of this patch of scales shows clearly that it is a character quite separate and distinct from the dark line of scales in the adult extending from it toward the base of the wing. The scales around the apex, yellow in the earlier stages, are now tipped with pale brown, but the outermost row of scales are still whitish as before. There is some deepening of the ground color just before the first and second pairs of streaks; the second dorsal streak, however, is the only streak which can be said to have acquired a definite margin, and even this is pale brownish. The basal streak remains entirely unmarginated.

In a specimen at a little later stage than that just described, internal margins, though very pale, have appeared along all of the white streaks; that of the second dorsal still continues to be in advance of the others. The margin of the first costal streak has deepened somewhat, and there is a faint suggestion of gray around its tip. A similar pale gray shade extends from the tip of the first dorsal streak through the middle of the wing and around the tip of the second dorsal streak. The ground color along the upper edge of the basal streak is somewhat darkened, but there is no margin.

In a wing at a considerably later period of development, the ground color approaches the adult color over those areas where there are no brown scales. The internal margins of the costal and dorsal streaks, as well as the upper margin of the basal streak, are dark brown; the external margins of these streaks and the margin around the tip of the basal streak while present are not as dark as in the adult and show a decidedly grayish tinge. This same gray color is prolonged from the tip of the first dorsal streak along the middle of the wing in the area formerly colorless but is much paler than in the adult. This difference from the adult color is especially noticeable above the patch of black scales, where in the imago there is a decided deepening of color, almost blending with the black patch. There is but very little deepening of color between the first and second dorsal streaks, and the margin of the second dorsal streak is neither as deep nor as wide as in the adult. The darkening of scales in the cilia started in earlier stages still continues. There is, however, no change from the colorless condition of the scales which are to be deep iridescent blue.

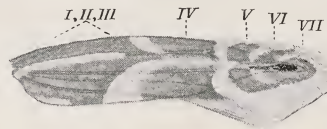


FIG. 13. Later stage in the development of color in the wing of *L. cratægella*.

The adult coloration appears to be attained several hours previous to emergence. At this time the markings are plainly visible through the pupal envelope. The bluish iridescence in the cilia is now well developed. Obviously this is one of the last characters to appear ontogenetically.

Lithocolletis ostryæfoliella Clem.

This species (Fig. 23, Pl. III) possesses an apical dot in its typical condition, composed of small black or blackish brown scales arranged in an almost circular shape over the tip of the wing.

In the youngest specimen examined, the wings were dissected out at a period when they were losing their whitish appearance and becoming faintly banded.

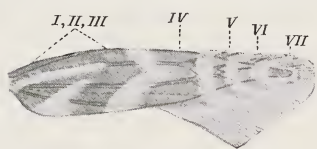


FIG. 14. Early stage in the development of color in the wing of *L. ostryæfoliella*.

The last four bands are straight and placed transversely on the wing, leaving colorless bands between them. The basal portion of the wing is exceedingly pale, and the ground color is scarcely discernible on the otherwise colorless wing. The configuration of the color areas is much the same as in the adult, there being the same outward angulation of Band III, internal to the first pair of white streaks. A stripe along the middle of the wing and a white spot on the dorsal margin remain colorless and mark the position of the basal streak and the white dorsal spot in the adult.

At a slightly later stage, the markings just referred to have become a little more distinct; the color is still a very pale straw (Fig. 14). The extreme base of the wing, while very pale, is still sufficiently contrasted with the unpigmented areas to show the outline of the basal streak defined for its whole length. On the dorsal edge, a pale shade broadest on the dorsal margin reaches two-thirds of the way across to the basal streak. On the basal side of this spot, the ground color seems a little deeper. Band III, although much angulated outwardly, is not yet connected in the middle of the wing with Band IV; thus the first pair of white streaks are still connected and form an angulated fascia, broadest at its extremities. Bands IV, V, VI and VII remain entirely separate and retain their primitive straight edges, with the exception of the inner edge of Band IV which has been somewhat produced toward the base at its extremities. Band III and Band VII are possibly a shade darker than the other portions of the wing; the scales attached around the apex projecting into the cilia are, however, paler and concolorous with Bands IV, V and VI.

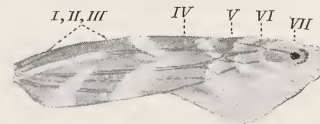


FIG. 15. Later stage in the development of color in the wing of *L. ostryæfoliella*.

The ground color continues to darken, reaching its adult condition at a relatively earlier stage than is the case in *L. cratægella*. At the same time (Fig. 15), the pale yellow spreads onto places originally unpigmented; thus the bands become connected by a paler yellow shade, so that the white fasciæ are transformed into pairs of opposite narrow white streaks. At this stage in the develop-

ment, there are four dorsal as well as four costal streaks. The apical dot is present, dark brown and almost as large as in the imago and very definitely outlined. Around the extreme apex, the scales projecting into the cilia are tipped with brown, this color being deepest just opposite the apical dot but quickly fading out on either side, so that it does not reach to the last pair of white streaks. The apical spot and these few scales around the apex are the only scales on the wing which show the slightest sign of brown; the bands are, however, a little deeper yellow on their outer than on their inner borders.

Very soon after the stage just described, the dark margin of the second dorsal streak begins to develop; at this time, it consists of a few darker and slightly grayish tinted scales somewhat removed from the dorsal margin. The apical spot is brownish black and seems to have reached its final development. The line in the cilia, though darkest immediately opposite the apical spot, is plainly visible from the fourth costal to the third dorsal streak, thus passing below the fourth dorsal streak which at this stage has almost disappeared owing to the fusion of Bands VI and VII.

Very little change is now needed to reach the adult condition. The margins of the second pair of white streaks continue somewhat in advance of the others and reach their final stage of development a little earlier. All trace of a fourth dorsal streak finally disappears.

Lithocolletis lucidicostella Clem.

At the time of the first appearance of a pale yellow tinge upon the wings, it is possible to discern faintly four bands in the apical half of the wing. Just before the apex within the area occupied by Band VII is a small colorless spot. With the exception of the fact that these four bands are not connected along the middle of the wing, the adult color areas (Fig. 44, Pl. III) are now laid down. The dorsal portion of Band IV, the most proximal of these four bands, is continued toward the base, as in the adult, by a pale yellow streak along the fold. Its costal portion is preceded by a white streak bordered internally by pale yellow which is extended along the upper median vein to the base.

The apical dot is the first dark mark to make its appearance. While the yellow is still very pale, the scales of the formerly colorless spot near the apex begin to take on a grayish tinge. The deepening of scales over this area seems to take place in very much the same manner as that of the dark scales before the apex in *L. cratægella*.

The apical spot continues to deepen and increase in extent, reaching its adult condition before there is any indication of the formation of dark margins. The development of the apical spot is accompanied by a gradual and uniform deepening of the ground color together with the fusion of all the bands in the middle of the wing and of VI and VII on the termen. The middle portions of the wing between the apices of the white spots are somewhat paler, showing where the pigment has recently appeared.

The darkening of scales in the cilia around the apex and just below it on the termen and the dark margins of the first costal and dorsal streaks are the next characters to appear. A wing examined at this stage shows the scales in the cilia brownish with scarcely a tinge of gray, the margin of the first dorsal streak somewhat paler and brownish yellow, extending from the cilia to vein 2, and the margin of the first costal streak pale and scarcely distinct. These observations are in agreement with those made on *L. cratægella* and *ostryæfoliella*; namely, that the dark markings appear earliest in the apex of the wing on Band VII and soon after on Band IV.

The process of development consists now merely of the gradual appearance and darkening of the margins of the other streaks and the extension of the line in the cilia to the first dorsal streak.

Lithocolletis morrisella Fitch.

At a period when the entire wing, viewed by transmitted light, seems uniformly colorless, the white markings as seen by reflected light are definitely laid down as they will appear in the adult (Fig. 48, Pl. III) and have already acquired the lustrous pearly tint characteristic of the adult. This white appearance is due entirely to the structural modification of the scales described earlier in this paper and cannot be in any way ascribed to a precocious development of the scales over these areas, since, when examined, all of the scales of the wing are seen to be fully developed.

With the first appearance of pigmentation, a pale yellow suffuses those portions of the wing only which are destined to be yellow in the adult (Fig. 16).

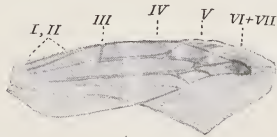


FIG. 16. Early stage in the development of color in the wing of *L. morrisella*.

In the basal half of the wing, therefore, the yellow is confined mainly to the region above the fold; there is, however, a faint yellow tinge just before the dorsal arm of the fascia. There is a scarcely discernible tinge of gray at the base of the dorsum below the basal streak and before the first dorsal streak. At the tip of the wing, over the area to be occupied by the apical dot, the scales are beginning to turn gray, those outermost being the deepest. Otherwise, the areas occupied by gray and black in the adult and by the white streaks appear by transmitted light uniform and colorless. Examination by reflected light shows that these two kinds of areas are not homologous, since the white streaks stand out clearly as structural modifications, while the scales margining them and those below the fold are duller and lack the pearly luster. The bands and the white fascia and streaks occupy their normal positions. The absence of a white streak over the apex of vein 7 is accounted for when it is seen that the apical spot has acquired such proportions as to cover the tip of vein 7, which in this and related species reaches the margin nearer to the apex than usual.

In the next stage examined (Fig. 17), the ground color has deepened somewhat, and decidedly more of the grayish tint has developed. The dorsal part

of the wing below the fold, to be occupied by black scales in the adult, is pale gray; beyond the fascia where the scales are merely brown tipped, the color is still yellow, concolorous with the rest of the wing. Internal and external margins of the streaks are beginning to form simultaneously, those of the first costal streak are the deepest. The change is direct from the colorless scales margining the white streaks to pale gray. The black streak in the fold beyond the fascia is at this stage composed of pale gray scales. The apical dot is still pale gray, but the outermost row of scales is much darker and continuous on either side with a line of gray scales extending from the fourth costal streak to the third dorsal streak. The scales whose tips are to form the dark line in the cilia are still white.

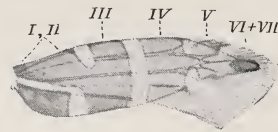


FIG. 17. Later stage in the development of color in the wing of *L. morrisella*.

On the next wing examined, the gray has decidedly deepened along the dorsal margin, but the golden color has not reached its final condition. The development of the margins has progressed considerably, but now the internal are decidedly in advance of the external margins. The former have a blackish color, especially toward the costal margin; the latter are still grayish. The external margin of the first costal streak is deeper than that of the others. The black streak in the fold has practically reached its adult condition. The apical dot has increased in size and color until its extent is now definitely defined. The scales around its outer edge, which in the preceding stage were the only dark ones, are now black. The line in the cilia is gray, but there is no indication of the bluish iridescence.

From this time on, no new characters appear, the development consisting only of a deepening of the colors to their adult condition.

The sequence of colors and the relative time of appearance of the various adult characters is very much the same in *L. robiniella* as in the species just studied. The apical spot and the black streak in the fold reach their final condition at a somewhat earlier stage in comparison with the development of the other markings.

Lithocolletis hageni F. and B.

This species (Fig. 17, Pl. III) possesses a well-defined apical dot, very decided external margins to the white streaks as well as the usual internal ones and a dark margin along the upper side of the basal streak. The margin along the upper side of the white basal patch is regarded as homologous with the margin of a basal streak, that along its outer side with the external margin of the white streak primitively separating Bands II and III. The streak of ground color beyond the basal white patch is, therefore, the dorsal portion of Band III.

Very few specimens of this species were available for study, but the observations confirm in general those made upon the five preceding species.

The apical dot appears well-defined and blackish at a period when Bands

V, VI and VII are still separated from one another by curved white fasciæ extending entirely across the wing and into the cilia (*Fig. 18*). The second pair of white streaks are still connected, but Band IV is beginning to project

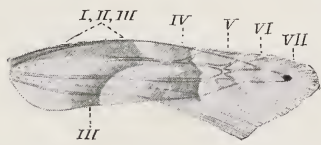


FIG. 18. Wing of *L. hageni* at the first appearance of the dark markings.

into them in the middle of the wing. At this time the ground color of the wing is a pale straw and lacks altogether the golden brown of the adult. The internal margins of the first and second dorsal streaks are beginning to form. The inner edges of the bands, bordering the streaks outwardly, present much the same appearance as they do in species where the white streaks never acquire external margins; that is, the ground color fades gradually into the white.

A dark line in the cilia begins to form soon after this; the scales showing the brown pigment at this time are not those which will be bluish iridescent in the imago; these latter remain pure white and only acquire their pigment later.

In the third specimen studied, the extent of the white streaks has been finally limited, and the golden brown color of the adult has been attained. All of the internal margins of the streaks, the dark scales at the apex of the first dorsal streak, those connecting the tips of the second pair of streaks and the two leaden-colored lines of scales running across the wing from the tips of the third and fourth costal streaks are present. In addition, external margins are present on the white basal patch and on the first dorsal streak. All of these borders are as they will appear in the adult. In this specimen, there was no indication of a deepening along the upper side of the basal patch. However, this observation cannot be accepted as altogether reliable in indicating the time of appearance of the margin of the basal streak, since the specimen was evidently abnormal, the apical dot not being present. No other specimens were available to decide the point. Imagoes of this species are occasionally found which lack both the apical dot and the dark margin along the upper side of the basal patch.

Lithocolletis æsculisella Cham.

The species heretofore studied have been those belonging to the group having cylindrical larvæ and characterized by the principal margins of the white streaks being internal. This species (*Fig. 70*, Pl. IV) and those following have the so-called flat type of larva, and the white streaks of the imagoes have their darkest margins on the outer side. That is, in the former group, the tendency is for the color bands to acquire first, dark margins on their outer edges; in the latter group, the condition is reversed, and the dark color appears first on the inner edges of the bands.

In *L. æsculisella*, at a period when there is scarcely any differentiation between ground color and bands, the pattern appears to be laid down almost as in the adult (*Fig. 19*). The bands are very pale buff, and judging from their uniform color, appeared simultaneously. The pale shade at the base which

separates Bands I and II extends entirely across the wing, but the early fusion of these bands on the costa is foreshadowed by the very faint tinge of buff just making its appearance in the costal portion of the pale fascia. On the extreme costa, Band V is indistinctly separated from VI. Band VI is separated from VII by a white streak extending entirely across the wing. With these exceptions, the yellow marks are defined as in the adult. The white oblique dorsal streak extends just within the termen, being separated from the white streak before the apex as in the adult. The distal end of the oblique dorsal streak is probably homologous with the middle portion of the white fascia which in primitive types separates Bands V and VI. In the imago, it sometimes exists as a separate small white spot before the apical dusting and more proximal than the oblique costal streak. Along the termen, the cilia are of an unbroken yellow color, showing that at the extreme margin, there has been a complete fusion of Bands V, VI and VII.

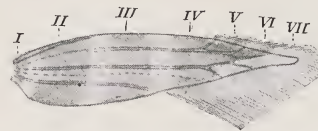


FIG. 19. Early stage in the development of color in the wing of *L. aesculisella*.

Before any of the dark margins begin to appear, the ground color deepens into the orange yellow of the adult. The external margin of the second fascia and the dark dusting at the extreme apex are considerably in advance of the other dark markings. The margin of the second fascia, formed by a dark line of scales along the inner border of Band IV, is most distinct in the middle portion of the wing and has not appeared on the extreme dorsal end nor on the costal end beyond the angle. Its color at this stage is brownish. In one specimen, the apical scales are not as dark as the margin of the second fascia; in another of the same age, as indicated by the state of development of the margins, the dusting of the apex is somewhat darker than the margin of this fascia; in both, however, the brownish tint is confined to the extreme apex. There is a slight darkening of the scales in the middle of the wing on the inner border of Band III adjacent to the first white fascia and along the under side of the oblique dorsal streak.

The dark margins of the fasciæ and of the oblique dorsal streak continue to develop, but before they reach their adult condition, the scales on the outer side of the costal spot over vein 10 begin to darken. At this time, the apical dusting is still confined to the apex of the wing and is not extended along the termen toward the tornus. This extension of the dusting toward the tornus is a characteristic of specimens appearing in the summer and does not occur in forms from overwintering chrysalids. It develops after the other adult characters have appeared.

Lithocolletis bethunella Cham.

In the youngest specimen examined, the ground color is a uniformly pale ochreous, and upon it the extent of the adult markings (Fig. 84, Pl. IV) is quite definitely blocked out (Fig. 20). The white fascia (or second pair of streaks)

is, however, prolonged outwardly at its angle along the wing to a position between the third pair of streaks. A comparison with the adult shows that the prolongation of the fascia is occupied by dusting on a whitish ground; that is, these

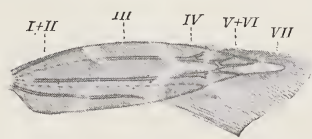


FIG. 20. Early stage in the development of color in the wing of *L. bethunella*.

white scales are destined to become black tipped. The third pair of streaks are situated normally over veins 10 and 2 respectively. There is no white spot over the tip of vein 9 on the costa. Bands V and VI have fused. A quadrate area in the apex remains colorless; the portion directly over vein 7 corresponds to the white streak normally situated here,

the remainder will be occupied by dark dusting in the adult. The scales around the margin at the apex are yellow; these in the adult will be brown tipped *yellow* scales.

In a wing at a somewhat later stage, there has been some deepening of the ground color. There is a small patch of scales just beyond vein 7 which are brown tipped and darker than any other scales on the wing. In the extreme apex, the scales extending over the cilia are not noticeably dark tipped. Dorsal to the dark patch of scales, the scales over the formerly colorless area become gradually paler, until near vein 5 their tips show just a faint tinge of gray. All the scales in the prolonged portion of the fascia are becoming pale gray tipped. There is also a faint gray tinge to the scales just below the tip of the dorsal arm of the fascia, continuous with the gray in the prolonged portion of the fascia. All of these scales are much paler than those in the apex just beyond vein 7 but approach in color those near vein 5.

The margins of the remaining streaks soon make their appearance; the dusting of the apex reaches the adult condition earliest.

A contrast in the sequence of development of dark marks is afforded by *L. caryæfoliella* Clem. In this species, the margins of the first and second fasciæ develop contemporaneously with a small patch of dusting at the extreme apex, and the margin of the second fascia is entirely complete, though not as dark as in the adult, at a stage when there is no indication of dark dusting beyond its angle. This dusting is very variable even in the adult, sometimes being very slight. The significance of the difference in development will be discussed later.

Lithocolletis ulmella Cham.

In this species, the pale yellow color appears simultaneously over all those areas which are to remain yellow in the adult (Fig. 95, Pl. IV) or in which the scales are *yellow* with brown or blackish tips. The white streaks and the white dusted portions of the wing remain colorless. Thus, the second costal streak is produced for a short distance along the cell, and the wing from vein 7 to the apex is colorless, but the scales around the apex and below the oblique dorsal streak, which are yellow with brown tips in the adult, have already acquired the pale yellow color.

In the next stage studied, the color has become almost as deep as in the adult. A number of the scales projecting from the extreme tip of the wing over the cilia are brown tipped; these are continued in a broken line through the cilia to the tornus. Over the wing membrane near the apex, in the area which was transparent in the earlier specimen, the scales are becoming dark tipped. These scales are deepest toward the apex of the wing, becoming very pale gray toward the tornus external to the oblique dorsal streak. A few scales along the costa corresponding in position with the dark scales in the adult are beginning to show darker tips. The scales margining the first and second costal streaks, which were whitish before, are now faintly gray. The color is uniformly developed over the whole margin and on the prolonged portion of the second streak.

In a specimen a little further advanced than the one just described, the apical dusting is almost as in the adult. This darker color does not quite reach the tornus; that is, the external edge of the white dorsal streak is still margined by pale gray scales as before. The margins of the first and second costal streaks have scarcely changed in color, but the scales in the prolonged portion of the second streak have darkened more rapidly; they are decidedly gray but much paler than those in the apex. The only new character which has appeared is the dark line through the cilia.

Lithocolletis hamadryadella Clem.

In the earliest stage examined (*Fig. 21*), the basal third of the wing is almost colorless. At the extreme base on the costal margin is a small patch of pale yellow scales, and a little beyond it another similar patch. These two patches of scales form Band I. Beyond these is a somewhat larger patch of pale yellow scales. This is the inner portion of Band II; the line of scales which marks its original outer limit in the adult (*Fig. 77, Pl. IV*) has not yet acquired any pigment. Band III at this stage is represented by a rather narrow angulated band which extends across the wing some distance before the tip of vein 1*b*. The white projects into its angle on the inner side. Band IV is composed of two separate patches of yellow scales, one on the costa and the other on the dorsum. Their pointed apices lie over the bases of veins 10 and 2 respectively, the normal position for Band IV, but on the margins, they curve back toward the base so that they are much farther removed from the tips of the veins than usual. The middle of the wing to the apex is colorless. Band V + VI is represented by a patch of scales on either margin. The dorsal patch originates just beyond vein 2 and extends over vein 5; the costal patch originates on the cell about midway between veins 10 and 9 but extends obliquely outward so that the inner edge on the costa is just basal to vein 9 and the outer edge just before vein 7. The white streak over the tip of vein 7 is very narrow, and its corresponding dorsal streak is indistinct. The

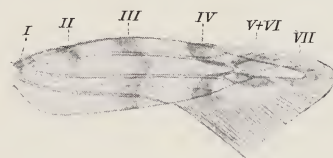


FIG. 21. Early stage in the development of color in the wing of *L. hamadryadella*.

cilia belonging to Band VII are all yellow with a few white scales here and there extending into them. Bands VII, V + VI and IV are somewhat deeper than Band III; Bands I and II are very pale, their paleness being caused by the large admixture of colorless scales at this stage.

In the next specimen examined, apart from a slight deepening of Band III and those beyond it, the only changes observed are the following. The two basal patches on the costa, belonging to Band I, show a slight admixture of brownish tipped white scales. The third patch (Band II) is now faintly continued to

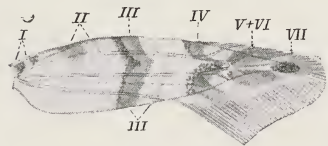


FIG. 22. Later stage in the development of color in the wing of *L. hamadryadella*.

the dorsum by a line of scattered yellow scales, and just beyond it, in the position normally occupied by the outer margin of Band II, is an angulated line of very faintly yellow scales. This marks the original outer limit (phylogenetically) of Band II. Just before the tip of vein 1b is a similar line of scales running parallel to the dorsal arm of Band III and marking its outer limit. These two lines of scales sometimes do not ap-

pear until a much later period in the development. Their time of appearance is largely determined by the number of yellow scales mingled with the dark scales in the adult, since it is only in the yellow scales that the pigment appears early.

In the next stage studied (*Fig. 22*), Bands I and II in the basal part of the wing remain practically unchanged. Band III is the same in extent, but its color has deepened. Its internal margin is beginning to form, the scales adjacent to the yellow becoming gray tipped. The gray pigment appears directly in the whitish uncolored scales of the previous stage without passing through any of the intermediate steps. In general, the margin is broadest on the costa, becoming narrower and paler below it, and not easily distinguishable toward the dorsum. On its inner edge, the margin is straight or slightly curved as in the imago; on its outer side, the scales project into the angle of the band and fill up the formerly colorless space. The tips of these scales are darker than those of the margin elsewhere. In this specimen, there are only a few scattered yellow scales beyond Band III and no indication whatever of the dark line of scales which is to appear later. The internal margin of Band IV is well marked on its dorsal half, consisting of several rows of dark tipped scales as in the imago. It curves between the two yellow patches, extending to their apices, but not beyond them into the colorless fascia. The costal half of the margin consists only of a few pale gray scales and does not quite reach the dorsal half of the margin. Except for a few very faintly grayish scales above the termen on the inner edge of the dorsal part of Band V + VI, there is no indication whatever of any darkening of scales adjacent to Band V + VI. Belonging to Band VII, and beginning just behind vein 7, the scales covering the entire apex of the wing are gray tipped. Some of them, especially on the costal margin, project over the yellow scales which are to form the line in the middle of the cilia. The gray tipped

scales of the apex, those between the two parts of Band IV and in the angle of Band III, are darker than the other scales forming the margins.

In a specimen at a considerably more advanced stage of development, the scales composing the two patches at the base of the costa are entirely gray tipped and very much the same as they will appear in the adult. The colorless scales mingled with those forming the proximal part of Band II are beginning to be gray tipped; this is especially noticeable on the quadrate part above the upper median vein; below it, there is only a line of a few scattered gray tipped scales reaching to the dorsum. The line of scales beyond, forming the original outer limit to Band II, is pale gray tipped throughout and, though broader on the costa, is complete to the dorsum. The broadening of the internal margin of Band III has continued. Its external margin, separated from the yellow band by white, is indicated by a single line of pale gray tipped scales running from the costa to the cell. The internal margin of Band IV has broadened and deepened and has now probably reached its adult condition. It is not possible to determine whether the development is completed in any single specimen, since there is a great deal of variation in the amount of dusting among the different individuals in this species. In this stage, the scales which in the imago are the most distal of those forming the dark external margin of Band IV are tipped with pale gray and connect with the dusting between the costal and dorsal parts of Band IV. Those on the inner side of the margin which will in a great measure fill up the white space between the margin and the yellow parts of the band are still uncolored. There is a very considerable patch of dusting internal to Band V + VI on the dorsal margin and connected with the apical dusting which has been extended proximally between the parts of V + VI. The costal dusting is not nearly as dark and is somewhat scattered. In addition to the extension of the apical dusting proximally, there has been an increase in the number of dark scales mingled with the cilia. The dark line through the middle of the cilia formed by brown tipped yellow scales is now quite distinct.

At this time, most of the dark markings are at least definitely defined in position; there is needed to bring them to their final state only a darkening of those scales already gray tipped and in some places the appearance of pigment in other scales adjacent to these.

In a specimen to be described now, most of these characters have appeared (Fig. 23). The patches of dark gray scales at the base of the costa and the line of scales beyond the third of these patches have increased and darkened decidedly. The line of scales external to Band III has now become dark gray tipped. External to Band IV, the dusting has been extended toward the base, so that only a small white streak is left between it and the band on the margins. The dusting in the apex has been much increased and extends along the margin, especially on the costa, and connects with the internal dusting of Band V, thus almost obliterating the white streak over vein 7.

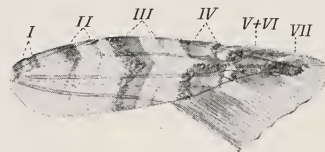


FIG. 23. Wing of *L. hamadryadella* near the end of the pupal state.

Cremastobombycia ignota F. and B.

In the youngest specimen examined, one in which the ground color was pale yellow, the extent and position of all the adult markings (Fig. 62, Pl. IV) is defined (Fig. 24). The paleness is especially marked toward the apex, where it is difficult

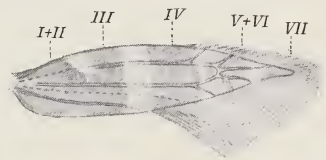


FIG. 24. Early stage in the development of color in the wing of *C. ignota*.

to distinguish the markings at all. The white fascia is considerably broader than it will appear later. A careful examination shows it to be composed of two parts, an inner fascia which is to form the white fascia of the adult and in which the scales are whiter and are fully formed, and an outer fascia, where the scales are not as large nor as well developed and are somewhat buffish in color. These scales will later form the black scales of the margin. This same thing is true of the other streaks but is not as noticeable except in the case of the first costal because of their more irregular shape. The band between the pair of streaks at three-fourths of the wing length and the streak enclosing the apex is, as shown by its position, equivalent to Band V + VI. The white streak before the apex is situated over the tip of vein 7.

In a later specimen, the ground color has deepened to that of the adult. The scales in the apex and in the cilia remain concolorous with the wing and are not darker at their tips. The dark external margins of the white fascia and streaks are appearing simultaneously, and all are equally advanced. The scales forming them correspond in position with the colorless scales which formed the outer part of the fascia in the preceding stage. The pigment, which is pale gray without a tinge of yellow or brown, is evenly distributed throughout the entire scale from the base to the tip. None of the internal margins has appeared.

In a later stage, the external margins are black as in the adult, and internal margins are present on the costal end of the first white streak and the fascia. There are no internal margins on the pair of streaks at three-fourths. As margins of these streaks are not always present in the imago, it is impossible to determine conclusively whether they normally appear after the internal margins of the fascia and the first streak. However, as will be shown later in the discussion, variable characters tend to appear later in the ontogeny than the fixed characters of a species.

The observations on the development of color in the wings of *C. solidaginis* (Fig. 60, Pl. IV) agree very closely with those on the preceding species. The configuration of the color areas at their first appearance is the same as that of the adult. In this species, however, the scales which are to form the dark margins in the adult are pale yellow instead of, as in *ignota*, being colorless and not fully formed. A comparison with the adult shows that these are dark tipped *yellow* scales, the dark pigment being found at the tip of the scales and not, as in *ignota*, almost uniformly distributed throughout the entire scale.

4. *Discussion and Conclusions.*

In general, I have found that the action of three processes is sufficient to explain the transformation of the seven primitive bands into the several existing patterns of the ground color. These three processes may be stated thus: (a) The middle portion of a band may be produced distally until it comes in contact with the band beyond it. (b) The extremities of a band may be broadened by being produced proximally. (c) The extremities of a band may be narrowed by the retraction of pigment from their outer edges. These three processes may act separately or in combination; the particular pattern produced is the resultant of their combined activity. The first two of these laws are based chiefly upon the changes observed during pupal development, the third law is deduced from adult characters, since the changes are such as cannot be observed directly. The evidence in detail is as follows:

In *L. tiliacella* (Fig. 7), seven distinct transverse bands of ground color are laid down; of these, those numbered II, III and IV appear first; following these, Band I, at the base of the wing, appears continuous in the costal half of the wing with II; it is, however, sufficiently separated from it by the difference in time of appearance. The three bands in the apex of the wing appear last and undergo no change; the connection of Band V with IV is brought about entirely by the extension outwardly of IV along the middle of the wing. The changes in Bands II and III are brought about by the spreading of the color onto areas formerly unpigmented; that is, the fascia between II and III is narrowed by the very slight growth *distally* of II along the *middle* of the wing, its extremities remaining fixed, and by the extension *proximally* of III, chiefly along the margins. Band IV reaches its adult configuration earliest; it is also the earliest to acquire the black pigment on its outer edge. This does not appear in the middle of the wing, where the band has extended outwardly uniting with V. The outer edges of the extremities of Band III have remained constant in position, and the dark scales appear first here. In Band II, there has been the least change in shape; the deepening of the pigment along its outer edge occurs more uniformly. From this, it follows that *while the general tendency is for dark pigment to develop along the outer edges of bands adjacent to unpigmented areas, the precise time of its appearance along any band or portion of a band in relation to other bands or portions of the same band is determined by the time when such bands or portions of bands reach their adult shape and color. The outer edge of a band in direct contact with another band acquires no dark pigment.* It would appear from the observations on this species that *the bands in their primitive condition are narrower than they are in the adult. A fascia may be narrowed by the uniform spreading of a band toward the base.*

These conclusions are corroborated by the observations on *L. tritæniarella* (Fig. 5, Pl. III); all the bands, however, appear simultaneously, and at this time all are straight. There is, however, a reduction in the apparent number of bands, V and VI being completely united. Band IV seems no further advanced than

the others toward the adult condition; as in *tiliacella*, development must take place more rapidly, since its margins reach their adult condition before those of the other bands. Here, also, is the first manifestation of that tendency, so characteristic of all the more highly differentiated species of the genus, toward the darkening of scales in the apex. In this species, these scales are scattered over the entire apex, instead of being limited to a definitely defined area where the scales are modified structurally. This species does not, at any stage, show the primitive type of marking; a considerable amount of development is, however, necessary before the color areas attain their definitive final extent.

In *L. cratægella* (Fig. 36, Pl. III), *ostryæfoliella* (Fig. 23, Pl. III), *lucidicostella* (Fig. 44, Pl. III), *hageni* (Fig. 17, Pl. III) and *morrisella* (Fig. 48, Pl. III), in the basal half of the wing, where in the adult there is the greatest divergence from a transversely banded type of marking, the color areas, upon the first appearance of a uniform pale yellowish, have almost exactly the same shape and extent as in the adult. They undergo very little change during development, except that in these species, as well as in *tiliacella* and *tritenianella*, there is a progressive and gradual deepening of the ground color. In the youngest specimens of *ostryæfoliella* observed (Fig. 14), the first pair of streaks are still connected; very soon, however, they become separated by the union of Band III with IV.

In the apical half of the wing, Bands V, VI and VII appear as straight transverse bands (except in *morrisella*); the transformation of the unpigmented fasciæ between them and between IV and V into pairs of opposite streaks is brought about by the outward extension of Bands IV, V and VI along the cell in a manner similar to that previously observed for Band IV in *tiliacella* and *tritenianella*. The obliteration of a white streak is brought about by the inward extension of the extremity of a band to meet the outer edge of the preceding band. In *morrisella*, the pattern is predetermined from the outset, the white fascia and streaks being produced by structurally modified scales, which are destined never to acquire pigment.

There are no reasons favoring the view that such a type of marking as that found in *cratægella* (Fig. 36, Pl. III) is primitive: there are many reasons for regarding it as having been produced through a long process of evolution. It is a matter of general observation that the pale colors appear first ontogenetically, black of the pigmental colors being last to appear; it has been inferred that the same is true also for the phylogeny. In the adults of these species, there have developed, in addition to the usual dark markings adjacent to the unpigmented areas, definitely limited black spots and streaks in the apex. The scales thus pigmented are also differentiated structurally from the surrounding scales by their smaller size. There is no such structural modification of the dark tipped scales in the apex of *tritenianella*. Obviously a considerable period of time must have been required for the final differentiation of such characters as these. That these species have undergone an extensive process of differentiation in the production of certain characters of a kind which can only be acquired late in

racial development, renders it highly probable that there has also been a far-reaching modification from the ancestral condition of the extent of the color areas. These phylogenetic changes are scarcely or not at all repeated in the ontogeny. Three primitive bands are still preserved during the early stages in the apex of the wing; the band proximal to these shows unmistakable signs of its origin from a straight transverse band, its outer edge being straight. We may, therefore, with reasonable certainty, conclude that the color pattern of the basal part of the wing may be traced back through a series of phyletic changes to its origin from the first three primitive bands.

The ontogeny offers no direct testimony of the means by which these results have been accomplished; it has given, however, visible evidence of two actual dynamic methods by which changes have been wrought; namely, *the middle portion of each band may be produced distally until it comes in contact with the band beyond it; the extremities of a band may be broadened by being produced proximally*. Thus are produced, first, angulated fasciæ; second, slightly oblique pairs of opposite streaks; the final effect of the second of the above processes, if acting alone, is the entire obliteration of the white streaks. That a third process has been at work is indicated by observations upon adult forms. The dorsal of the first pair of white streaks in *L. cratægella* (Fig. 36, Pl. III) does not occupy its primitive position over vein 1b but has been displaced toward the base, and vein 1b reaches the margin within Band IV; that is, there has been an extension of the extremity of Band IV in this direction over the area formerly white. But since a white streak still remains, there must have been a compensating drawing away of the outer edge of Band III at its extremity. Such a withdrawal of pigment cannot, of course, be observed ontogenetically. A third dynamic process in the transformation may, therefore, be stated thus: *the extremities of a band may be narrowed by the retraction of pigment from their outer edges*. This is an example of the shrinking away of a band at one end. In this case, the shrinking takes place at the *outer* edge of the band only. The result of the combined action of the second and third of these processes is the progressive movement of the end of the band toward the base.

These three processes are sufficient to explain the origin of all the types of marking in this genus; the specific results in any case are due to the manner and extent of their action; that is, whether they act singly or together and to the relative rapidity of action of the three processes. How they have combined to produce these various types will be discussed in detail under the heading of phylogenetic development.

In the second division of the genus, the extent of the areas of ground color undergoes very little change during development. The ground color appears in the earliest stages over those areas which in the adult are occupied by *yellow* or *reddish yellow* scales or by dark tipped *yellow* scales. The scales, which in the adult are white with dark brown, gray or black tips, do not receive pigment until much later; they then pass directly to gray or brownish gray and thence to

black, without passing through the intermediate yellowish and brownish shades. The tendency for dark pigment to develop along the edges of bands adjacent to unpigmented areas is exemplified in this group also, with this difference, however, that it appears first along the *inner* edge of a band. When dark pigment develops in addition along the outer edge, it appears at a later period. The converse is true in the first division of the genus; the dark margin appears earlier on the *outer* side of a band. I can offer no explanation of the original cause of the difference in direction of development; the result in either case seems to be the expression of the same general tendency in development, acting, however, with different degrees of intensity on either side of a band. It would seem that the development of unusually dark pigment on one side of a band—the acceleration of chemical processes over a localized area—retards development on the other side.

The ontogeny within this division affords very little evidence of the operation of the first two processes of evolution defined earlier in this discussion. However, the shape of the bands and the separation of the white fasciæ into opposite spots, with the total obliteration of some of the spots, is sufficient proof that these forces have acted during the evolution of the species.

L. hamadryadella (Fig. 77, Pl. IV) alone, of those observed, shows the outward prolongation of the middle of a band; the gradual extension distally of the dark dusting between the dorsal and costal portions of Band V + VI and its final contact with the apical dusting (Figs. 22, 23) is an example of the working of this law. The third law postulated to explain the displacement of oblique streaks toward the base receives decisive confirmation from the adult markings of the same species. A narrow line of scales crosses the wing beyond the yellow portions of each of Bands II, III and IV, being separated from them by white. These scales occupy positions corresponding to the outer margins of these bands; ontogenetically, the dark pigment develops in them after it has appeared on the inner margins of these bands. The conclusion is apparent that these lines of scales mark the earlier phylogenetic limits of these bands. The bands have shrunk away, most rapidly on the costa and dorsum, leaving behind them the margins as visible evidences of the process.

In *L. tiliacella* (Fig. 7), which, from its conservation of the greatest number of bands in a primitive straight condition, the very pale ground color and the entire absence of any dark scales in some of the bands, may be regarded as the most primitive of the American species, there is a difference in the time of appearance of the bands. In the more advanced species, the bands appear at the same time. Evidently, then, in the higher species, there is a hastening and crowding together of the earlier stages, so that the bands which formerly appeared in sequence now appear contemporaneously. Those in the apex of the wing, which have experienced the least modification during the phylogenetic development of the species, alone recapitulate the racial history during their ontogenetic development.

The discussion heretofore has dealt chiefly with the processes which effect the final limitation and configuration of the *ground color*. The general tendency toward the production of dark pigment in rows of scales adjacent to unpigmented areas has also been noted. These streaks of dark scales, which are usually transverse, and the various other characteristics, such as the apical spot, the longitudinal streak of black scales in the apex and the black streak in the fold, properly constitute the *markings*, in distinction to the ground color, and are superimposed upon it. While the progressive change in the configuration of the ground color is the important factor in determining the *general evolution* of the *genus* and the different stages at which development has halted form the *starting points* for the differentiation of the different *groups* of species, the development of the markings is the important factor in determining the phylogenetic sequence of the *individual species* within each group. A knowledge of their mode of origin and relative time of appearance is therefore essential.

In *L. tiliacella* and *tritænianella*, it was seen that the dark margin develops first along the edge of Band IV, which is the first band to reach its adult shape. In *L. tiliacella*, the outer edge of this band has become fixed before all of the bands have even been laid down. The dark margin appears toward the costa and dorsum, in places where the outer edges of the band have undergone no change whatever since the first appearance of color. The dorsal margin seems to be in advance of the costal. There is no darkening of pigment along the bands in the apex, which appear comparatively late. From these observations, it appears that *in the ontogeny, the dark margin develops earliest along the edge of that band which first reaches its definitive adult condition. Before dark margins can develop, the edge of a band must have remained fixed for an appreciable period of time.*

In *L. cratægella*, *ostryæfoliella* and *lucidicostella*, the dark margin on Band IV is also the first to appear. The apparent contradiction to the principle just laid down that a dark margin develops earliest along the edge of the band that has first reached its definitive adult condition, lies in the fact that in these species the color areas in the basal half of the wing are at the outset defined almost as in the adult, while the bands in the apex repeat the racial development. It might be expected, then, that the margin would appear earliest along the first pair of streaks. It has, however, required a much longer time in the *evolution of the species* for the basal half of the wing than for the apical half of the wing to acquire its present aspect; the development in the apical half has come to a standstill comparatively early in the phylogenetic history of the species. The observed recapitulation in the apical three or four bands during the ontogenetic development of the steps in the racial differentiation of the species is in harmony with the conclusions of other investigators that it is only among primitive forms that anything approaching a complete repetition of phylogenetic changes is to be found in the ontogeny.

The apex of the wing (in respect to the conservation of primitive color areas) may be regarded as primitive in comparison to the base of the wing. In

the phylogenetic development of this type of marking, therefore, it is possible that the margins appeared on Band IV while the basal half of the wing was still under the influence of dynamic forces producing constant changes in the outlines of the areas of ground color. No margins could have appeared in the basal half of the wing until after these outlines had become permanent. Some of these changes, as has been already shown, are such as cannot be repeated during pupal development. Hence the color areas in the basal half of the wing tend to be laid down in their final shape. *The sequence of the appearance of dark markings, which are in reality a second series of transverse bands superimposed upon an earlier set, follows the same order for the ontogeny as for the phylogeny; that is, in this second and more recent set of characters, there is an actual recapitulation.* The margins of Bands V and VI appear later, corresponding, therefore, to the sequence in the time of appearance of these bands phylogenetically, hypothetically based upon that of *L. tiliacella*. The margin on the upper side of the basal streak corresponds in time to the outer margins of the bands; it appears before inner margins develop. An *outer* margin of a band tends to appear first near the *costa* or *dorsum*, an *inner* margin near the *middle* of the wing; that is, at the apex of the outer side of a white streak, these being the parts of the edges of the bands which have reached their permanent position earliest. Therefore, *the relative time of appearance of the dark margin of any band in the ontogeny is dependent upon the time when the edge of that band became fixed in the phylogeny.*

In *L. morrisella* (Fig. 48, Pl. III), margins are formed almost simultaneously on either side of the white streaks by a direct change to gray and thence to black. The pigment in the other black scales develops in a similar manner without passing through the usual intermediate stages. The gray and black pigments make their first appearance at an early stage, while the ground color is still pale yellow. The structural differentiation of the white scales, the massing of black scales in the dorsal half of the wing, the exceedingly large apical spot and the black longitudinal streak in the fold all indicate the very high phylogenetic position of this species. Upon the addition of these newer characters, the earlier ones were crowded closer together and pushed farther back into the ontogeny, resulting in their contemporaneous development.

In the species of the second division of the genus, dark margins develop in conformity with the principles already enunciated. There are certain minor differences between this and the preceding division attendant upon the original unexplained diversity in the inherent tendencies of the two divisions. The dark margin appears first on Band IV in the middle of its inner edge, in contrast to its appearance in the other division on the outer side and near each end of this band; the same is true for Band III. This is a necessary consequence of the action of the three general processes of evolution; *the middle of the inner edge of any band remains stationary, and hence a margin will develop here earlier than at the extremities of the band.*

In *Cremastobombycia ignota* (Fig. 62, Pl. IV), the development is very similar

to that of the species of the "flat-larval group." The margins appear almost simultaneously, the scales changing directly from colorless to gray and thence to black. These scales, at the time the yellow ground color spreads over the wing, are not fully formed, thus contrasting with the similarly unpigmented, but fully developed scales belonging to the white fascia and streaks. In all other species examined, the scales were all equally and fully formed at the time of the first appearance of pigment in any part of the wing.

In many species, these dark streaks adjacent to white are the only defined dark markings present; there may be a few scattered, darker tipped scales in the apex. An increase in the amount of dark pigment producing additional dark markings manifests itself in either of two ways. (1) The *number* of scales thus affected may be increased, so that the actual extent of the wing occupied by dark tipped scales is greater. This is the direction that evolution has taken in the species of the "flat-larval group" (illustrated on Plate IV) and in a few of the species of the "cylindrical-larval group" (*e. g.*, *celtisella*, Fig. 56, Pl. III, and *celtifoliella*, Fig. 4, Pl. III). Often, among the more highly differentiated of the species of the "flat-larval group," the entire apex of the wing is covered with black tipped scales (*e. g.*, *agrifoliella*, Fig. 79, Pl. IV). Similar areas may develop in other parts of the wing; thus a patch of dark tipped scales may extend outwards from the angle of a fascia (*e. g.*, *bethunella*, Fig. 84, Pl. IV). (2) There may be a *concentration* of pigment in comparatively few scales, which with increasing differentiation tend to be segregated in definitely limited areas marked out by structural modifications of the scales (*e. g.*, *lucidicostella*, Fig. 44, Pl. III, and *cratægella*, Fig. 36, Pl. III). In these cases, the scales are pigmented almost to their bases, not merely dark tipped. With the single exception of *obstrictella* (Fig. 64, Pl. IV) among the species of the second division of the genus, this tendency is confined to the species of the "cylindrical-larval group," where it manifests itself in the apex either as an apical dot or as a somewhat elongate or irregular patch of scales, broadest just before the tip of the wing. A similar longitudinal streak of black scales is present in the fold in *robiniella* (Fig. 50, Pl. III), *uhlerella* (Fig. 49, Pl. III), and *morrisella* (Fig. 48, Pl. III).

Finally, there may be a decided deepening of the ground color itself between the white streaks. This process has reached its highest development in *robiniella*, *uhlerella*, and *morrisella*.

In the ontogeny, the development of all of these specializations has been much abridged, and concomitant with this, their time of appearance has been pushed back farther and farther into the earlier stages of pupal development. The dark tipped scales remain colorless during the time the yellow scales are attaining their adult condition; later, they change directly to gray and black. The pigment in the areas of dark tipped scales in the apex and beyond the fasciæ often appears simultaneously with that of the margins. Some variation is to be noticed here; in *L. bethunella*, the gray pigment appears in all the scales beyond the fascia, simultaneously with the *beginning* of the formation of the dark

margin; in *L. caryæfoliella*, the dark margin of the fascia is *complete* before any pigment has developed in the area beyond it. In the imago, the patch of dusting beyond the fascia is an established constant character in *bethunella*; in *caryæfoliella*, the amount of such dusting is very variable, indicating its recent appearance in the species.

It would seem then that *only those characters permanently established and of long standing in a species exhibit this precocity of development; recently acquired or variable characters appear ontogenetically in the order of their phylogenetic sequence.*

This conclusion is confirmed by observations upon the mode of development ontogenetically of other analogous dark markings. Comparison of imagoes indicates that the apical spot and the black patch in the apex have originated phylogenetically earlier than the streak of brown scales along the middle of the wing but later than the dark internal margins of the white fasciæ and streaks. In *L. cratægella*, the pigment in the scales of the black patch before the apex, which is unquestionably a characteristic only acquired through differentiation extending over a long period of time, appears earlier than that in the brown scales extending along the middle of the wing and reaches its definitive adult condition while the latter are still wholly unpigmented. In *L. hageni* also, the apical spot appears sooner than the dark scales in the middle of the wing beyond the tip of the first dorsal streak.

Such specializations as these cannot, however, have originated very early in the evolution of a species, and the observed phenomenon of their unduly precocious appearance and rapid development in the ontogeny requires additional explanation. In *L. cratægella*, *ostryæfoliella*, *lucidicostella*, *hageni* and *morrisella*, these were the first dark markings to appear. The first tinge of gray appeared before the ground color itself had reached its adult shade or rarely even before it had reached its adult configuration. It is possible that physiological causes act directly toward this end. In the racial development, the segregation of black scales over a limited area and the later modification of these scales structurally has been accomplished gradually; the results have become permanent in the species, and the scales, when first formed before any pigment has entered them, have a structure identical with that acquired late in phylogenetic development. It is suggested, in explanation of the phenomenon of the early appearance of black pigment in them, that the concentration of pigment-forming substances within a smaller space—the interior of these smaller scales—results in a more intense chemical action over a localized area and thus hastens development.

The general conclusions which have been drawn from the study of pupal development may be summarized as follows:

1. The primitive type of color pattern consists of a series of seven transverse bands, which, except the first, cross the wing perpendicular to the costal margin and are not wider than the unpigmented fasciæ between them. Their positions are determined by the course of the longitudinal nervures.

2. In the evolution of the genus, changes in extent alone of bands are

brought about by the uniform spreading of the pigment toward the base, the edges of the bands remaining straight. Changes in the extent and form of these bands have taken place through the action of any or all of the three following dynamic processes: (a) The middle portion of a band may be produced distally until it comes in contact with the band beyond it. (b) The extremities of a band may be broadened by being produced proximally. (c) The extremities of a band may be narrowed by the retraction of pigment from their outer edges. The action of the first two may be observed directly, the third is an inference from a comparison of adult markings.

3. The bands, either in their primitive shape or as modified through the course of evolution, constitute the ground color upon which a second darker series of transverse characters is superimposed. These are properly termed the markings and appear at the limits between ground color and unpigmented areas. Their relative time of appearance, ontogenetically, is dependent upon the time when that portion of the edge of a band has become fixed phylogenetically.

4. Later in the phylogenetic history, spots and longitudinal black markings may appear. For reasons not fully understood, certain of these markings appear earliest in the ontogeny.

5. Recapitulation in the ontogeny is at most only partial and is confined to those species or to those parts of the wings in which there has been the least advance from a primitive condition. Here also a distinction must be made between ground color and markings.

(e) PHYLOGENETIC DEVELOPMENT OF THE COLOR PATTERN.

From the previous discussion, it was seen that a few definite processes, identical in all of the species, have acted to produce modifications in the extent and configuration of the areas of ground color. Later, a set of darker transverse markings has been superimposed upon the ground color. The dark pigment appears in rows of scales contiguous to unpigmented areas. There are two possibilities in regard to the place of its first appearance, namely, the outer or the inner edge of a band.

While the evolution of the pattern of the *ground color* has taken place in the same directions in both divisions and in the two subgenera of the genus, the development of the dark markings has followed different directions. In the division whose larvæ are of the ordinary cylindrical type and in *Porphyrosela*, the dark markings appeared first on the outer edges of the bands; in the division whose larvæ are of the modified flat type and in *Cremastobombycia*, the margins appeared first on the inner edges of the bands.

Two different inherent tendencies in development are therefore exhibited. These two lines of development must have diverged early in the phylogeny, while the only color pattern was still that blocked out on the white wing by the shape of the areas of ground color and before any of the dark markings had appeared, since neither type of marking can be derived from the other, and the

species of the first division are more closely related among themselves than to any of the species of the second division or of *Cremastobombycia*.

An ancestral form, more primitive in respect to generic structure as well as color pattern and transversely marked with seven bands of a uniform pale yellowish color, has evidently given rise first to a series of species in which dark margins have developed earliest on the outer edges of bands—in this case, the white streaks and fasciæ are said to be internally dark margined. Later, or perhaps contemporaneously, in another species of the same ancestral strain, the opposite tendency has developed, and there has been evolved a series of species in which dark margins appear earliest on the inner edges of the bands—in this case, the white streaks and fasciæ are said to be externally dark margined. A few of these latter species, constituting the subgenus *Cremastobombycia*, have retained a more primitive generic structure; the remainder have followed the same course of evolution structurally as the species of the first division of the genus. It is, of course, possible that this second tendency originated twice and independently.

Several factors combine to render it probable that *Cremastobombycia* (in its modern form) and the "flat-larval group" originated at a somewhat later period than the typical *Lithocolletis* (Fig. 26). The restricted geographical range of the "flat-larval group" and of *Cremastobombycia*, which with one exception are confined to America, indicates their comparatively recent origin. Considerations based upon larval characters confirm this view. The later larval stages of the typical *Lithocolletis* are identical with those of *Gracilaria*, which is without question accepted as the ancestor of all these groups. The corresponding stages in the larva of *Cremastobombycia* have a more flattened and triangular-shaped head, without, however, the structural modifications which have developed in the "flat-larval group." It may be concluded, then, with reasonable certainty, that after the origin of the typical *Lithocolletis*, the species of the ancestral stock retained for a short period their imaginal structure. During this time, changes in the larval form were initiated. In the ancestral form of *Cremastobombycia*, development along this line did not progress far, and the larvæ have preserved the normal mode of feeding; hence there has been no attendant structural modification.

Cremastobombycia may have originated after a certain amount of evolution in the color pattern had already taken place; this view is supported by the observation that none of its species conserves as primitive a type of marking as is to be found in several species of the "flat-larval group."

We may conclude, therefore, that the immediate ancestor of all the groups under discussion was of a somewhat more primitive structure than *Cremastobombycia* as we now know it. The structural relations of the four groups with reference to the ancestral stem are illustrated diagrammatically by Fig. 25; the relative time of origin of each by Fig. 26. The similarity of the color pattern of the species of *Cremastobombycia* to that of some of the species of the second

division of the genus does not in any way indicate that this is primitive; it has rather been produced independently in the two groups, by the action of the same three fundamental factors.

The phylogenetic tree thus shows two main stems extending in different directions from a common origin. By the application of the three general principles directing the evolution of the pattern of the ground color, it is possible

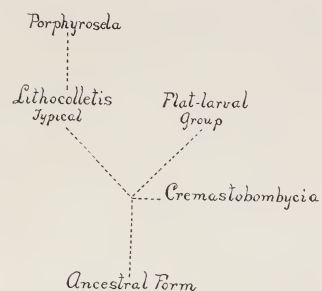


FIG. 25. Phylogenetic tree showing structural relationships of the groups of *Lithocolletis*.

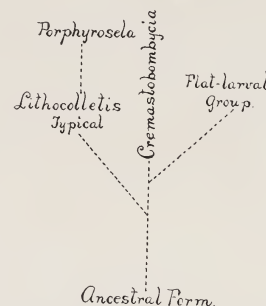


FIG. 26. Phylogenetic tree showing relative time of origin of the groups of *Lithocolletis*.

to retrace the steps in the origin of the different groups of species. The evolution of the species of the "cylindrical-larval group," which will be discussed first, is illustrated on Plate III.

In all of the species except *bataviella* (Fig. 58), there has been a fusion of Bands I and II along the costa.

If evolution in the shape of Bands II and III has been in the same direction and at the same rate, and the outward growth of the middle of each has not been sufficient to bring it in contact with the band following, and this outward growth has been compensated for by an equal growth toward the base of the extremities of Bands III and IV, species characterized by two entire fasciæ will be produced, the first at the basal fourth, the second at the middle of the wing.

Where evolution ceases early, all or most of the bands may be preserved as transverse bands. *L. tiliacella* (Fig. 1) has been differentiated as a species when, except for the fusion of I and II on the costa, Band IV alone had come in contact with the band beyond. Specific differentiation, that is, the production of dark margins, etc., has also halted soon, as we observe that no dark scales are present on the last three bands. If development along the same line proceeds farther, and by the farther outward growth of the middles of Bands II and III and the extension inwardly of the extremities of III and IV, the fasciæ between them become distinctly bent, the pattern of the ground color resembles that of *oregonensis*. There has also been an accompanying gradual deepening of the ground color. Specific differentiation at this level over a long period, as evidenced by the black apical spot, has given rise to *oregonensis* (Fig. 2). If, on the other hand, evolution of the first three bands stops at the level of *tiliacella* but continues in the apical four bands until IV, V, VI and VII are continuous along the middle of the wing, species of the type of the European *L. nicellii* will be produced.

If the bands continue to become more and more bent outwardly and the fasciæ between them gradually narrowed, forms of the type of *fragilella* (Fig. 3) will be produced. If now the action of the third law comes into play, the outer edges of the bands on the margins will move toward the base; if the extremities of the bands are extended toward the base at the same rate, very acutely angled fasciæ will result, as in *celtifoliella* (Fig. 4).

If the extension of the ground color toward the base in Band VI has taken place rapidly, there is an entire obliteration of white between V and VI, which then form a single uniformly colored band. In *tritænianella* (Fig. 5), *affinis* (Fig. 6) and *ostensackenella* (Fig. 7), this has occurred, Bands II, III and IV remaining nearly straight. In *mariaella* (Fig. 8), these bands have become bent outwardly. In *ostensackenella*, while the bands have remained straight, there has been a very decided advance and specialization in other directions; namely, in the structural modification of the scales forming the fasciæ and spots and in the darkening of the base of the wing into a deep brown except near the base of the dorsum. There has also been considerable modification in the larva, which has become more flattened and in which the sides of the segments project more prominently than usual. It also deviates from the typical habits of the genus in that it leaves the mine to pupate.

We may regard *Porphyrosela* as having originated from an ancestor with this type of marking. The recent origin of the species within it (Fig. 9) is indicated by the deep ground color, dark margins on either side of the white fasciæ and the structural modification of the white and the purple scales.

If the extension distally of each of the bands along the cell has continued until it has reached the band beyond and the inner extremities of the bands have been produced basally at a slower rate, the result is the production of pairs of opposite white streaks.

In *auronitens* (Fig. 10), it is probable that the fasciæ were considerably narrowed before these processes began, thus accounting for the almost perpendicular position of the white streaks.

In the remaining groups of species, these processes began early and the pairs of streaks are more or less oblique. There is first produced a form in which the ground color is blocked out as in *argentinotella* (Fig. 11). *Occitanica* (Fig. 12) is derived from *argentinotella* by the obliteration of the first, fourth and fifth costal streaks.

If now a movement of the extremities of each band toward the base is accompanied by a corresponding extension of the extremities of the band beyond it toward the base, very oblique white streaks result. Where these movements have taken place at an approximately equal rate in all of the bands, forms such as *leucothorax* (Fig. 13) will be produced. The outer edge of Band II on the costa has been retracted completely to the base so that the first white costal streak begins at the base. This species furnishes further evidence of the long continuance of evolution by the well developed apical spot.

If on the dorsal margin, the retraction of pigment from the outer edge of Band III takes place more rapidly than the extension proximally of the extremity of that band, its dorsal portion will disappear, and the second white dorsal streak will coalesce with the first; *fitchella* (Fig. 14) typifies this result. The extension of color onto a white streak has probably taken place most rapidly just within the dorsal margin; the evidence for this conclusion rests upon the observed concavity of the outer edges of the white streaks and their greater width on the margin.

If the most rapid movement, as is usually the case, has been that of the outer edge of Band II toward the base, the first result will be the union of the upper inner edge of the first white dorsal streak with the short oblique streak at the base separating Bands I and II. A small streak of ground color will be left between them on the dorsum; this soon becomes a small spot removed from the dorsal margin by the more rapid shrinking away of Band II on the margin. *Salicifoliella* (Fig. 15) and *tremuloidiella* (Fig. 16) have been differentiated as species at this level.

The small spot of ground color just referred to becomes smaller and smaller and finally disappears. The base of the dorsal margin is then occupied by a white patch whose outer edge is the inner edge of Band III. Differentiation at this stage has given rise to *hageni* (Fig. 17), *arbutusella* (Fig. 18) and *insignis* (one variety) (Fig. 19). In *hageni* and *insignis*, the first white costal streak has disappeared entirely. Following closely behind the retraction of pigment from the outer edge of Band II on the costa, the extremity of Band III has been produced along the costa to the base; phylogenetically then, this is the second time pigment has appeared along the base of the costa. In *arbutusella* (Fig. 17) the first costal streak has been involved in a change similar to that of the first dorsal with which it has united. In these three species equally distinct dark margins have appeared on either side of the white streaks, and there has been a very decided darkening of the scales of the ground color between the streaks, indicating that after the general phylogenetic evolution of the pattern of the ground color had come to a standstill, specific differentiation proceeded rapidly and for a considerable period of time. In the other variety of *insignis* (Fig. 20), Band III in its dorsal half has been produced to the base, most rapidly just above the dorsum, leaving a white median basal streak and a white spot on the dorsum near the base. This then is the method by which a median long basal streak has originated; its basal part is therefore homologous with the white streak separating Bands I and II; its apical half is homologous with a part of the white streak separating the dorsal portions of Bands II and III.

Where the extension of Band III to the base has followed immediately on the progressive withdrawal of pigment from the outer edge of Band II, without the intervening cessation in development found in *insignis*, the configuration of the color areas is that of the group of species of which *obscuricostella* (Fig. 25) and *crataegella* (Fig. 36) are typical examples. In most of the species of this

group, there has also been a retraction of pigment from the outer edge of Band III, and at the same time, the extremities of Band IV have been produced toward the base so that the first pair of white streaks are very oblique and are situated before the tip of vein 1b which in more primitive forms determines the position of these white marks. The obliteration of the first white costal streak has not been attained in all the forms which reached this level before evolution in the pattern of the ground color halted and species differentiation began, since it is preserved in some species and lost in others.

Within this group the development of the dark markings in the apex has taken two different directions; the black marking in the apex may take the form of a round apical dot, or of a streak or patch of black scales of variable shape. Of the species with apical dots, *caryæalbella* (Fig. 21) lags somewhat behind the other species; the suffusion of the base of the wing with pale yellow is not yet complete, but the first costal streak has been lost. Development has been more rapid toward the costa than in the dorsal half of the wing; the converse is true for *rileyella* (Fig. 22) where the first white costal streak remains. In conformity with the principle that within a group a darker ground color and the presence of dark markings indicate a higher phylogenetic position, the sequence of the remaining species with an apical dot will be *ostryæfoliella* (Fig. 23), *olivæformis* (Fig. 24), *obscuricostella* (Fig. 25) and *kearfottella* (Fig. 26). In the last two species all trace of a white spot near the base of the dorsum has vanished.

Of the species characterized by more or less irregular patches of black scales in the apex, *populiella* (Fig. 27) is probably the most primitive from the point of view both of color areas and markings. Among several of the species, namely, *diaphanella* (Fig. 28), *salicivorella* (Fig. 29), *deceptusella* (Fig. 30), *alni* (Fig. 31) and *alnicolella* (Fig. 32), the pair of streaks in the middle of the wing are not very oblique, that is, there has been a more restricted action of the last two of the three processes of evolution than is observed in the five following species. In *ledella* (Fig. 33), *incanella* (Fig. 34), *scudderella* (Fig. 35), *cratægella* (Fig. 36), *malimalifoliella* (Fig. 37) and *propinquinella* (Fig. 38), these streaks are very oblique.

If evolution of the pattern of the ground color, instead of halting at the level of the preceding group of species, proceeds farther, it takes place in two directions.

1. The base of the wing may be uniformly suffused with ground color, so that no white streaks remain when evolution ceases, and therefore no dark markings develop. The configuration of the ground color in the remainder of the wing has remained constant during these changes. This is the condition of affairs in *sexnotella* (Fig. 39), *æriferella* (Fig. 40) and *obsoleta* (Fig. 41). In *obsoleta* the pattern remained fixed for a short time, and the development of dark pigment in the scales adjacent to the white streaks was initiated, then the extension of all the bands toward the base was resumed, checking further develop-

ment of dark pigment. The result is a tendency toward a uniform distribution of ground color over the entire wing.

It may be objected that the color pattern of the three species just discussed could have been derived directly and in a more simple manner from that of *L. argentinotella* (Fig. 11) by the broadening of the extremities of Bands II and III toward the base, resulting in the obliteration of the white streaks separating Band I from II and Band II from III. On this hypothesis the greater changes have occurred in the middle of the wing since the oblique pair of streaks in the middle of the wing have been produced by the combined action of the second and third processes of evolution. This is not in agreement with the facts observed up to this stage in the evolution of the color pattern, namely, that the greatest changes have occurred near the base of the wing, nor with the general principle that development is more rapid in the more proximal parts of an organism.

2. The shrinking away of the ground color at the extremities of the bands may continue and the outer edges of Band III may be involved to a greater extent than hitherto observed. In *albanotella* (Fig. 42) evolution in this direction has ceased comparatively early, the darker ground color and heavier dark margins indicating the longer time occupied in specific differentiation. In *argentifimbriella* (Fig. 43) the withdrawal of color from the base of the wing has been almost complete and there has been no later extension of color toward the base from Band IV. In *lucidicostella* (Fig. 44) there is a slight extension of color along the dorsal margin; the halting in development has been too recent for a dark line of scales to develop on the streak of ground color extending along the upper side of the cell. In *clemensella* (Fig. 45) this streak has also disappeared. In the four preceding species, evolution has taken place more rapidly on the dorsal than on the costal margin of the wing. In *quercialbella* (Fig. 46) and *trinotella* (Fig. 47) the costal half of Band III has also shrunk away; the only transverse bands then remaining are the four apical ones. In the European fauna, the final consummation of this process is witnessed in such species as *L. cramerella* and *L. tenella*. Development has halted at different levels, as in our species, and dark streaks have appeared at the edges of the bands. Gradually then bands more and more distal have shrunk away, leaving behind them the dark fuscous streaks on an almost white ground.

In all of the groups whose evolution has been traced, modification in the shape of Bands II and III, in the early phases of evolution has progressed in the same direction and at approximately equal rates, so that the bands are of similar shape (cf. *argentinotella*, Fig. 11).

In the following species evolution has proceeded independently in each of these bands.

Changes may proceed very slowly on the inner edge of Band IV and outer edge of Band III; the tendency is then toward the preservation of a median

white fascia. If the outward growth of Band II along the cell is comparatively rapid, a pair of opposite streaks will be produced at the basal fourth. These changes have taken place very early in the phylogenetic history, and if evolution of the pattern of the ground color ceases here, species of the type of *morrisella* (Fig. 48), *uhlerella* (Fig. 49) and *robiniella* (Fig. 50) will develop. The laws governing specific differentiation have had an opportunity to operate over a long period of time, and very highly specialized individual characters have developed. In *robiniella* evolution of the pattern did not cease quite as soon as in the other two species, the fascia has been narrowly separated into two streaks and all of the streaks have become more oblique. In consequence of the later beginning of specific differentiation, the individual characters are not as highly specialized as in *uhlerella* and *morrisella*.

If the edges of the first pair of streaks move toward the base, and there is no corresponding extension of the extremities of Band III toward the base, species of the type of *lucetiella* (Fig. 51) will be produced.

Where Band III has been extended to the base, there is a basal streak very similar to that of *cratægella* (Fig. 36) and the other species of that group. *Martiella* (Fig. 52), *gemmea* (Fig. 53) and *symphoricarpella* (Fig. 54) have originated thus. In *symphoricarpella* the basal streak is very small—the ground color has shortened and narrowed it.

If the outer edge of Band III instead of remaining straight has grown distally along the cell and at the same time the movement of its extremities toward the base has been accompanied by a compensating extension of the extremities of Band IV toward the base, angulated fasciæ will result; *apicinigrella* (Figs. 55a, 55b) and *celtisella* (Fig. 56) have been thus differentiated. Finally this angulated fascia may become very acutely angled through the shrinking away of Band III and the white may be extended along the margins to the base of the wing. At this stage a very slight outward growth of the middle of Band III will divide the fascia into very oblique streaks; *basistrigella* (Fig. 57) has been thus produced. In this species the separation of a white fascia into a pair of streaks was the last step in evolution; in the other species characterized by opposite streaks, this process has been one of the earliest events in evolution.

Bataviella (Fig. 58) is an early isolated offshoot from the main stem; it alone of all the species has preserved, in some of its varieties, Band I at the base of the wing distinctly separate from II. Specific differentiation has extended over a length of time sufficient for all of the scales of the ground color to become dark tipped.

The second main stem of the phylogenetic tree, which has given rise to *Cremastobombycia* and the "flat-larval group," is illustrated on Plate IV.

The species of *Cremastobombycia* and of the "flat-larval group" have followed very similar lines of development. In *Cremastobombycia* the result has been modified somewhat by the shorter and very oblique, almost horizontal position of the white streak separating Bands I and II. A white basal streak

when formed is therefore nearer the dorsal margin. The chief forces acting in the evolution of the pattern in this subgenus are the more rapid growth distad of Band II as compared with Band III and the extension proximad of the extremities of Bands III and IV. The sequence of the species is as follows: *grindeliella* (Figs. 59a, 59b), *solidaginis* (Fig. 60), *ambrosiella* (Fig. 61), *ignota* (Fig. 62), *verbesinella* (Fig. 63). *Grindeliella* shows the basal streak in actual process of formation; where the dorsal arm of the first fascia is wanting, the black scales at the tip of the basal streak are homologous with those on the outer margin of the fascia. All show the tendency which arises independently throughout the "flat-larval group" also, toward the complete fusion of Bands V and VI. None of these species can be regarded as very primitive. The similarity to a group of species in the division of the genus shortly to be discussed is due to the fact that the same laws underlie their evolution.

A tendency similar to that witnessed among several of the species of the first division of the genus, toward the preservation of Bands II and III in a shape approaching the primitive, prevails among many of the species of the second division of the genus. *Obstrictella* (Fig. 64) has preserved Bands II, III and IV in a very primitive condition; during its differentiation, however, the white streak at the base has been entirely obliterated.

Above this level, evolution takes place in four divergent directions, as represented on Plate IV.

In one of these branches, Bands II, III and IV tend to remain separate. Within this group, the first step in evolution is the outward extension of the middle of Band IV to meet Band V; at the same time the bands become displaced very slightly toward the base of the dorsum; the fasciæ between them are not as yet angulated. Specific differentiation at this level has produced *tubiferella* (Fig. 65), in which all white markings beyond the fasciæ, except sometimes a minute white dot before the apex, have been suffused with ground color; *aceriella* (Fig. 66) and *hamameliella* (Fig. 67), the latter more advanced because of its deeper ground color; *ostyrella* (Fig. 68), *corylisella* (Fig. 69), *æsculisella* (Fig. 70) and *guttifinitella* (Fig. 71). The loss of the white streak at the base seems to be accomplished after the principal changes in the configuration of the ground color have been brought about, that is, after specific differentiation has set in. The fact that the white streak extends entirely across the wing, separating Bands I and II completely in such species as *hamadryadella* (Fig. 77) and *umbellulariæ* (Fig. 78) which are by no means primitive in regard to the shape of the areas of ground color, and observations on the development of color in the pupal wings of *æsculisella*, support this hypothesis.

In *caryæfoliella* (Fig. 72) and *lentella* (Fig. 73), the bands have become quite distinctly though obtusely angulated.

Above this level evolution has taken divergent paths. In one direction, evolution in the shape of Bands II, III and IV has progressed in the same manner

and at the same rate, so that although the fasciæ between them have become acutely angled, they have remained parallel. *Macrocarpella* (Fig. 74) and *cinnaminiella* (Fig. 75) have been differentiated at this level. These two species are characterized by an unusual number of dark tipped scales; the fasciæ are also internally dark margined near the costa. In *saccharella* (Fig. 76) evolution has continued farther, and other changes of a different character have resulted. There has been a slight displacement of the dorsal oblique streaks toward the base; the first of these is brought into contact with the basal streak. The costal portion of the first fascia has been replaced by the ground color.

In the other direction, where evolution has progressed at a more rapid rate on the outer edge of Band III and inner edge of Band IV, than on the outer and inner edges of Bands II and III respectively, the second fascia will be more acutely angled and its arms more oblique than the first fascia. Such is the condition in *hamadryadella* (Fig. 77), *umbellulariæ* (Fig. 78) and *agrifoliella* (Fig. 79). In the first of these there is but little divergence in direction of the two fasciæ, evolution in this direction having halted comparatively early. Specific differentiation progressed rapidly and dark pigment developed along the outer as well as the inner edges of the bands. At this stage regressive changes have commenced; the bands have shrunk away toward the base, most rapidly at the extremities, but also in the middle, leaving behind them the lines of dark scales which marked their former outer edges. In *umbellulariæ* and *agrifoliella*, progressive evolution continued longer, and the arms of the second fascia are very oblique compared with those of the first. Specific differentiation has continued longer in *agrifoliella* than in *umbellulariæ*; the recent disappearance of the white fascia separating Bands I and II is shown by the presence of black scales external to its normal position and by the occasional presence of a few pale scales anterior to them.

In all of these species characterized by two white fasciæ, there is a tendency toward a disproportionate acceleration of the outward extension of the bands along the cell, with the attendant result that the fasciæ are often interrupted at the angle.

In a collateral line of development, there has been an early acceleration in the processes of evolution affecting the outer edge of Band II and the inner edge of Band III. As a result Band II becomes fused with Band III over a considerable space in the middle of the wing, at a period when III and IV are still separated from one another by an angulated fascia. *Fletcherella* (Fig. 80), *arcuella* (Fig. 81), *betulivora* (Fig. 82), *australisella* (Fig. 83), *bethunella* (Fig. 84), *chambersella* (Fig. 85), *cervina* (Fig. 86), *platanoidiella* (Fig. 87), *castaneæella* (Fig. 88) and *fasciella* (Fig. 89) have followed this path of evolution. *Chambersella* (Fig. 85), *cervina* (Fig. 86) and *platanoidiella* (Fig. 87) have been differentiated subsequent to the first five species; fusion of Bands II and III has been complete in the dorsal half of the wing.

In *castaneæella* (Fig. 88) and *fasciella* (Fig. 89), evolution has progressed more slowly on the outer edge of Band III and inner edge of Band IV; the median fascia remains almost straight, but the other white markings have almost disappeared.

In two species, *nemoris* (Fig. 90) and *gaultheriella* (Fig. 91), the relations between the progressive changes in Bands II and III have been reversed. The tendency here is toward a fusion of Bands III and IV earlier than II and III, with the result that the second fascia is separated into opposite spots earlier than the first. *Gaultheriella* is the more advanced of these two species.

In all of the groups whose evolution has just been traced, the action of the third process of evolution, namely, the retraction of pigment from the outer edges of the extremities of bands, has been of minor importance. In the evolution of four species, *mediodorsella* (Fig. 92), *quercivorella* (Fig. 93), *conglomeratella* (Fig. 94) and *ulmella* (Fig. 95), the characteristic longitudinal white streak has originated through the action of this process at the extreme dorsal end of each of Bands II, III and IV in sequence, followed by the extension of color toward the base from Bands III and IV, just within the dorsal margin. This is analagous to the process which has occurred in species of the first division of the genus, where it was observed that the most rapid extension of a band into the white streak preceding it took place just within the margin. These processes occur first near the base, then the bands more and more distad are involved. In *mediodorsella* (Fig. 92) Band IV has not yet been produced toward the base to obliterate the dorsal arm of the median fascia; in *quercivorella* (Fig. 93) this advance has been made. In *conglomeratella* (Fig. 94) and *ulmella* (Fig. 95), the regressive changes have been extended to Band IV, which has shrunk away on the margin, allowing the white oblique streak to move proximally along the margin until it has united with the more proximal portion of the longitudinal streak. This theory of the origin of the longitudinal dorso-basal white streak is substantiated by the variations in its width. It is widest at points corresponding to the original extremities of the white fasciæ, and narrowest immediately behind them.

From the foregoing account of the evolution of the groups and species of *Lithocolletis*, it is evident that the general evolution of the pattern of the ground color may halt at any level and the species differentiated at this level constitute a natural group of species more closely related to one another than to any other species. The level at which evolution has come to a standstill is no absolute criterion of the age of the individual species within a group. A species with but few specialized specific characters in a group whose color pattern marks it as of recent origin may be older phylogenetically than one of a more primitive group, where the high degree of specific differentiation attained marks it as of recent origin. It is to be expected that the most highly differentiated species, that is, those where the darker colors predominate both as regards ground color and markings, would be found in groups where the pattern of the ground color has a

less degree of modification; the earlier evolution in this direction has halted, the longer will have been the time available for specific differentiation. On the other hand, species belonging to groups recently established and hence of high phylogenetic position, may be almost lacking in the darker colors. Actual examples of each of these possibilities are furnished among our species; *morrisella* (Fig. 48, Pl. III) and *fragilella* (Fig. 3, Pl. III) are examples of the first, *quercialbella* (Fig. 46, Pl. III) of the second possibility.

III. GENERAL DISCUSSION.

Ontogenetic and phylogenetic studies upon the development of the color pattern in *Lithocolletis* lead to the conclusion that evolution has taken place in definite directions under the action of a few definite laws; in other words, that it has been orthogenetic. It was shown that the primitive color pattern, the first to be laid down upon the white wing, is a series of seven uniformly colored, pale yellow transverse bands. From these, the color areas, which form the *ground color* of the various groups of species, have been derived. The first tendency observed is a uniform widening of the bands. Evolution in the shape and extent of the primitive bands of ground color, as has been shown (see page 141), has been brought about by three definite processes, two of which were observed in actual operation in the development of color in the pupal wings; the third is a necessary inference from the lack of agreement between the primitive positions of the bands and their positions in the more advanced species. The most far-reaching and widespread changes have taken place toward the base of the wing proximal to the transverse vein.

The final result of the action of these three processes is a uniform ground color; this uniformity will be attained first near the base of the wing, since it is here that evolution has proceeded most rapidly. The color bands in the apical half of the wing, which were laid down later, are modified at a slower rate and retain more nearly their primitive shape. These observations are in agreement with the general principle that development is more rapid in the anterior and proximal parts of an organism.

The observed evolution in the pattern of the ground color suggests that *the uniform yellowish ground color which suffuses the wing in the higher Lepidoptera, beginning at the base and spreading distalward, is the outcome of a phylogenetically older type of marking, originally banded, and later fused to a uniform color, and that the markings are a second series superimposed upon the first.*

If the disposal of the transverse primitive bands of ground color is dependent upon the positions of the nervures, as my observations on *Lithocolletis* have indicated, then in the primitive color pattern of the ancestral Lepidoptera where more veins are present and their arrangement on the margins is more symmetrical, the number of these bands should be considerably augmented. As evolution has proceeded, this primitive type of color pattern would have been modified in various ways. Attendant upon the degradation in venation in some

of the lower groups, there must have been immediate and complete fusion of bands occupying adjacent interspaces, when the vein which separated them was lost. Modification in the shape of the wings, resulting in changes in the relative positions of the nervures, must also have been an important factor in producing correlated changes in the primitive color pattern by bringing about displacement and fusion of some of the bands. Just what modifications in the color pattern would have been produced by the direct action of these conditions, could only be determined by a complete knowledge of the actual series of changes which have taken place in the wings of Lepidoptera. Beyond, and apparently independent of these factors, there is the evolution in the shape and extent of the color areas themselves.

It was found that dark markings, properly so-called, appeared at the limits between ground color and unpigmented areas. Increase in breadth of a dark marking takes place away from an unpigmented area. The dark markings do not appear until the edge of a color area has remained constant for an appreciable length of time. Since they appear at the edges of color areas, their shape and position are in great part determined by the same laws which control the evolution of the pattern of the ground color. Markings once formed tend to become permanent and immovable. Thus we find that the suffusion of an unpigmented area with ground color subsequent to the formation of a dark streak does not affect its permanency; the shrinking away of ground color leaves a dark streak or line isolated in an otherwise unpigmented area. Therefore, *although, during the early stages of evolution, the development of markings was entirely dependent on the configuration of the ground color, these markings once permanently established in the race, tend to reappear independently of the ground color. When this level has been reached in racial history, we have a series of transverse markings appearing on a uniform ground color.* This is the condition in all of the higher Lepidoptera. In the ontogeny of such groups, there is no evidence to show that these markings are a second series superimposed upon the earlier primitive one.

If the theory of the origin of dark markings on opposite edges of primitive bands of ground color is a valid one, we should expect to find in the higher types, that there is a tendency for dark stripes to recur in pairs, and that fusions at any single period would be more apt to occur between any *two* consecutive stripes than between three consecutive stripes. Observations confirm this hypothesis. Among many of the Pyralids, the dark markings are formed of two dark lines connected by a paler color; each of these marks is separated from a similar pair of lines by ground color. Even in the butterflies, the tendency toward grouping of dark marks in pairs is witnessed. Eimer's ('97) series of adult forms of *Papilio* and von Linden's ('98, '02) figures of the pupal development illustrate this principle. In the pupal development of the wings of *Papilio machaon*, the tendency for the dark scales to appear first at the edges of bands was noted; bands thus formed have, on my hypothesis, originated from the fusion of dark stripes situated on either side of a primitive band.

The great diversity to be observed in the position, shape and extent of the dark markings in the various groups of Lepidoptera, is due to differences in the direction of evolution of the pattern of the ground color, and the different levels at which it has halted, permitting the dark markings to develop.

The actual appearance of dark pigment in certain defined positions is probably due to physiological factors; just why these processes should occur contiguous to unpigmented areas is largely a matter of conjecture. It is possible that the chemical changes involved are oxidative in their nature; the presence of air in the unpigmented hollow scales may possibly accelerate chemical processes along this line. This supposition will however not account for the phylogenetic permanency of such markings after the ground color covers the wing uniformly.

The investigations of previous workers upon the color patterns of Lepidoptera have been limited to the markings, that is, to that series which I have designated as secondary and superimposed upon an original primary color pattern. In as much, however, as these markings have originally been determined by the configuration of the pattern of the ground color, the laws concerning their places of appearance should agree with my observations on the evolution of the pattern of the ground color; it is on the contrary not to be expected that these laws concerning behavior of the markings will apply in their entirety to the comparatively primitive and phylogenetically older type of markings in this genus. The laws governing the color pattern have been based upon more highly developed markings often of comparatively recent origin phylogenetically. For convenience in comparison a statement of some of these laws of coloration follows. The following are those advanced by Mayer ('97):

“(a) Any spot found upon the wings of a moth or butterfly tends to be bilaterally symmetrical, both as regards form and color, the axis of symmetry being a line passing through the center of the interspace in which the spot is found, and parallel to the direction of the longitudinal nervures. (b) Spots tend to appear not in one interspace only, but as a row occupying homologous places in successive interspaces. Indeed we almost always find spots arranged in linear series, each similar in shape and color to the others and occupying the center of its interspace. (c) It is interesting to notice that bands of color are often made by the fusion of a row of adjacent spots; and conversely, chains of spots are often formed by the breaking up of bands, leaving a row of spots occupying the interspaces. (d) The most common method of disappearance is a shrinking away of the band at one end. It is very common to find bands shrinking away at one end. This is a special case of Bateson's law that the ends of a linear series are more variable than the middle. Sometimes however they shrink away at both ends, and very often, they break up into a row of spots, which may then contract into the centers of their interspaces and finally disappear. It is worthy of note that it is very rare to find a band breaking at the middle of its length and each half receding from the other. (e) The position of

spots which are situated near the edge of the wing is largely controlled by the wing-folds or creases."

Eimer has derived the various types of coloration from a series of transverse stripes (termed by him longitudinal because parallel to the longitudinal axis of the body) which break up into spots which fuse crosswise to form markings parallel to the longitudinal nervures, and finally fuse to a uniform color. New markings appear on the body of the animal from behind forwards and from above downwards, or conversely, whilst the old ones disappear in the same direction and succession.

I have shown that the ground color has been derived from a series of such transverse elements; conversion into a uniform color has taken place directly by an extension of color onto previously unpigmented areas, distad through the middle of the wing in the cell, proximad on the margins. The positions of the markings are arbitrarily determined. They are dependent upon the level at which evolution in the pattern of the ground color acting in a few definite directions has come to a standstill. The actual appearance of the markings is probably due to physiological activities whose nature is not understood. The first markings are usually transverse, rarely longitudinal when the modification in the ground color has been far-reaching. These transverse markings are in the nature of narrow lines or streaks, phylogenetically the forerunners of the bands of higher Lepidoptera. *Since the streaks and lines of dark scales in Lithocolletis still retain their primitive condition as originally laid down, it is not to be expected that the laws which Mayer has given, based upon the transformation of spots and bands in the higher Lepidoptera, would find wide application in this group.* Portions of a pair of such streaks in *Lithocolletis* will be found at the margins and in each interspace which the band from which they are derived crosses. Breaking up of bands formed by the growing together of these streaks will result in conditions such as Mayer has described for spots and series of spots. Any spot such as the apical spot is bilaterally symmetrical and occupies the center of its interspace. The primitive bands from which the ground color has been derived and which have been regarded as a primary set of markings upon which a second set, the markings proper, have been superimposed, have exhibited the tendency toward shrinking away at each end.

The ultimate causes which determine the definitive positions of the primitive bands are unknown. Von Linden has found that in the lower orders of insects, the coloring matter has a tendency to collect on transverse veins; this however does not bring us any nearer to a real explanation of the phenomenon of coloration. The probability that the origin of the markings, which appear secondarily, may be traced directly to physiological factors, renders it reasonable that the appearance of the primary series is conditioned by like physiological and morphological factors within the organism itself and is independent of external factors.

Evolution in the pattern of the primitive series of bands has been shown to have taken place in a few definite directions; the diverse patterns which have

been produced are the result of different combinations of three general processes already discussed.

IV. SUMMARY.

Observations on the development of color in the pupal wings and a comparison of the color pattern in adult forms of *Lithocolletis* have shown that in this group the primitive color pattern is a series of seven uniformly colored pale, yellow transverse bands, separated from one another by unpigmented areas. The disposal of these bands is dependent upon the course of the longitudinal nervures, since the points of origin or the tips of the veins mark the positions of the unpigmented fasciæ between the bands.

From this primitive color pattern, the several different types of color pattern in this genus have been derived. Evolution has taken place in definite directions, under the action of three general processes, which were found to be sufficient to explain the origin of the different color patterns. These processes have been stated thus: (a) The middle portion of a band may be produced distally until it comes in contact with the band beyond it. (b) The extremities of a band may be broadened by being produced proximally. (c) The extremities of a band may be narrowed by the retraction of pigment from their outer edges. The particular result in any case, that is, the configuration of the color areas, is due to the manner and extent of the action of these processes.

During pupal development, these phylogenetic changes are repeated only to a very limited extent; recapitulation is confined to those species or to those portions of the wing in which there has been the least modification of the primitive transversely banded type of marking.

These bands either in their primitive or modified shape, constitute the ground color. Upon this ground color, a second darker series of elements, the markings proper, also usually transverse, are superimposed. The different levels at which evolution in the pattern of the ground color has halted, that is, the configuration of the areas of ground color, are the important factors in determining the phylogenetic sequence of large groups; the particular colors and the markings determine the positions of the species within those groups.

These markings appear at the limits between ground color and unpigmented areas, as one or more lines of dark scales along the edge of a band adjacent to a white fascia or streak. Their appearance then is probably due to physiological factors within the organism itself, and is independent of external conditions. In the ontogeny, the relative time of appearance of the dark margin of any band is dependent upon the time when the edge of that band became fixed in the phylogeny. Before dark margins can develop, the edge of a band must have remained fixed for an appreciable time. Hence, where bands have been laid down late or have reached their present configuration late in racial development, the dark margin will develop at a correspondingly late period in ontogenetic development.

This principle holds good irrespective of whether or not there is a recapitulation of phylogenetic changes in the configuration of the color areas during pupal development. Therefore in the second and more recent set of characters, there is an actual recapitulation. A dark marking once permanently established in the race tends to reappear independently of the ground color, so that later suffusion of the unpigmented area contiguous to it with ground color, or the shrinking away of the ground color, does not affect its permanency.

Later in phylogenetic history, additional dark markings, other than those contiguous to unpigmented areas, may appear. The development of these characters in the pupa becomes much abridged, and concomitant with this, their time of appearance is pushed back into the earlier stages of pupal development, so that they may appear simultaneously with or even earlier than characters which are much older phylogenetically. However, only those characters permanently established and of long standing in a species exhibit this precocity of development; recently acquired or variable characters appear ontogenetically in the order of their phylogenetic sequence. Where certain characters appear unduly early in pupal development, physiological factors probably act directly in bringing about this result.

From a study of the phylogeny of the various groups of species, through the application of the processes of evolution already enumerated, it was found that the most far-reaching and widespread changes have taken place toward the base of the wing, proximal to the transverse vein. The final result is the production of a uniform ground color which will be attained earliest near the base of the wing where evolution has proceeded most rapidly.

This observed evolution in the pattern of the ground color suggests that the uniform yellowish ground color which suffuses the wing in the higher Lepidoptera, beginning at the base and spreading distalward, is the outcome of a phylogenetically older type of marking, originally banded, and later fused to a uniform color, and that the markings are a second series superimposed upon the first.

The observations made clearly point to the conclusion that the evolution of the color pattern in *Lithocolletis* has been orthogenetic.

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EXPLANATION OF PLATES III AND IV.

PLATE III.

Phylogenetic tree illustrating the evolution of the species of the "cylindrical-larval group" of *Lithocolletis* and of *Porphyrosela*. (The figures on this and the following plate are three times natural size.)

- FIG. 1. *Lithocolletis tiliacella* Cham.
 FIG. 2. " *oregonensis* Wlsm. (not illustrated).
 FIG. 3. " *fragilella* F. and B.
 FIG. 4. " *cellifoliella* Cham.
 FIG. 5. " *tritenianella* Cham.
 FIG. 6. " *affinis* F. and B. (not illustrated).
 FIG. 7. " *ostensackenella* Fitch.
 FIG. 8. " *maricella* Cham.
 FIG. 9. *Porphyrosela desmodiella* Clem.
 FIG. 10. *Lithocolletis auronitens* F. and B.
 FIG. 11. " *argentinotella* Clem.
 FIG. 12. " *occitanica* F. and B. (not illustrated).
 FIG. 13. " *leucothorax* Wlsm.
 FIG. 14. " *fitchella* Clem.
 FIG. 15. " *salicifoliella* Clem.
 FIG. 16. " *tremuloidiella* Braun.
 FIG. 17. " *hageni* F. and B.
 FIG. 18. " *arbutusella* Braun.
 FIG. 19. " *insignis* Wlsm. (not illustrated).
 FIG. 20. " *insignis* Wlsm.
 FIG. 21. " *caryæalbella* Cham.
 FIG. 22. " *rileyella* Cham.
 FIG. 23. " *ostryæfoliella* Clem.
 FIG. 24. " *olivæformis* Braun.
 FIG. 25. " *obscuricostella* Clem.
 FIG. 26. " *kearfottella* Braun.
 FIG. 27. " *populiella* Cham.
 FIG. 28. " *diaphanella* F. and B.
 FIG. 29. " *salicivorella* Braun.
 FIG. 30. " *decepusella* Cham.
 FIG. 31. " *alni* Wlsm. (not illustrated).
 FIG. 32. " *alnicoella* Wlsm.
 FIG. 33. " *ledella* Wlsm.
 FIG. 34. " *incanella* Wlsm.
 FIG. 35. " *scudderella* F. and B.
 FIG. 36. " *cratægella* Clem.
 FIG. 37. " *matimalifoliella* Braun.
 FIG. 38. " *propinquella* Braun.
 FIG. 39. " *sexnotella* Cham.
 FIG. 40. " *aeriferella* Clem.
 FIG. 41. " *obsoleta* F. and B.
 FIG. 42. " *albanotella* Cham.
 FIG. 43. " *argentifimbriella* Clem.
 FIG. 44. " *lucidicostella* Clem.
 FIG. 45. " *clemensella* Cham.
 FIG. 46. " *quercialbella* Fitch.
 FIG. 47. " *trinotella* Braun.
 FIG. 48. " *morrisella* Fitch.
 FIG. 49. " *uhlerella* Fitch.
 FIG. 50. " *robiniella* Clem.
 FIG. 51. " *lucetiella* Clem.
 FIG. 52. " *martiella* Braun.
 FIG. 53. " *gemmea* F. and B.
 FIG. 54. " *symphoricarpella* Cham.
 FIG. 55a. " *apicinigrella* Braun.
 FIG. 55b. " *apicinigrella* Braun.
 FIG. 56. " *celtisella* Cham.
 FIG. 57. " *basistrigella* Clem.
 FIG. 58. " *bataviella* Braun.

PLATE IV.

Phylogenetic tree illustrating the evolution of the species of *Cremastobombycia* and of the "flat-larval group" of *Lithocolletis*.

- FIG. 59a. *Cremastobombycia grindeliella* Wlsm.
 FIG. 59b. " *grindeliella* Wlsm.
 FIG. 60. " *solidaginis* F. and B.
 FIG. 61. " *ambrosiella* Cham.
 FIG. 62. " *ignota* F. and B.
 FIG. 63. " *verbesinella* Busck.
 FIG. 64. *Lithocolletis obstrictella* Clem.
 FIG. 65. " *tubiferella* Clem.
 FIG. 66. " *aceriella* Clem.
 FIG. 67. " *hamameliella* Busck.
 FIG. 68. " *ostryarella* Cham.
 FIG. 69. " *corylisella* Cham.
 FIG. 70. " *æsculisella* Cham.
 FIG. 71. " *guttifinitella* Clem.
 FIG. 72. " *caryæfoliella* Clem.
 FIG. 73. " *lentella* Braun.
 FIG. 74. " *macrocarpella* F. and B.
 FIG. 75. " *cincinnatiella* Cham.
 FIG. 76. " *saccharella* Braun.
 FIG. 77. " *hamadryadella* Clem.
 FIG. 78. " *umbellulariæ* Wlsm.
 FIG. 79. " *agrifoliella* Braun.
 FIG. 80. " *fletcherella* Braun.
 FIG. 81. " *arcuella* Braun.
 FIG. 82. " *betulivora* Wlsm.
 FIG. 83. " *australisella* Cham.
 FIG. 84. " *bethunella* Cham.
 FIG. 85. " *chambersella* Wlsm.
 FIG. 86. " *cervina* Wlsm.
 FIG. 87. " *platanoidiella* Braun.
 FIG. 88. " *castaneæella* Cham.
 FIG. 89. " *fasciella* Wlsm.
 FIG. 90. " *nemoris* Wlsm.
 FIG. 91. " *gaultheriella* Wlsm.
 FIG. 92. " *mediodorsella* Braun.
 FIG. 93. " *quercivorella* Cham.
 FIG. 94. " *conglomeratella* Zell.
 FIG. 95. " *ulmella* Cham.

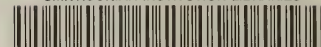


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